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MISSOURI BOTANICAL GARDEN

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ANNOUNCEMENTS
The Dennis Stanfield Award 234
The 1982 Jesse M. Greenman Award 234
ATSATT, PETER R. & PHILLIP RUNDEL. Pollinator Maintenance vs. Fruit Production: Partitioned Reproductive Effort in Subdioecious *Fuchsia lycioides* 199
BAKER, H. G. & I. BAKER. Starchy and Starchless Pollen in the Onagraceae 748
BAKER, I. (See H. G. Baker & I. Baker) 748
BERRY, PAUL E. (See Dennis E. Breedlove, Paul E. Berry & Peter H. Raven) 209
BERRY, PAUL E. The Systematics and Evolution of *Fuchsia* Sect. *Fuchsia* (Onagraceae) 1
BOUFFORD, DAVID E. The Systematics and Evolution of *Circaea* (Onagraceae) 804
BREEDLOVE, DENNIS E., PAUL E. BERRY & PETER H. RAVEN. The Mexican and Central American Species of *Fuchsia* (Onagraceae) except for Sect. *Encliandra* 209
CARLQUIST, SHERWIN. Wood Anatomy of Onagraceae: Further species; root anatomy; significance of vestured pits and allied structures in Dicotyledons 755
CONEY, PETER J. Plate Tectonic Constraints on the Biogeography of Middle America and the Caribbean Region 432
CROSS, AUREAL T. & RALPH E. TAGGART. Causes of Short-term Sequential Changes in Fossil Plant Assemblages: Some Considerations Based on a Miocene Flora of the Northwest United States 676
EYDE, RICHARD H. Evolution and Systematics of the Onagraceae: Floral Anatomy 735
GENTRY, ALWYN H. Neotropical Floristic Diversity: Phytogeographical Connections Between Central and South America, Pleistocene Climatic Fluctuations, or an Accident of the Andean Orogeny? 557
GOLDBLATT, PETER. Corm Morphology in *Hesperantha* (Iridaceae, Ixioideae) and a Proposed Infrageneric Taxonomy 370
GOLDBLATT, PETER. Notes on *Geissorhiza* (Iridaceae): The Species in Madagascar 379
GOLDBLATT, PETER. A Synopsis of *Moraea* (Iridaceae) with New Taxa, Transfers, and Notes 351

GÓMEZ P., LUIS D. The Origin of the Pteridophyte Flora of Central America 548

GRAYUM, MICHAEL H. (See Barry E. Hammel & Michael H. Grayum) 420

HAMMEL, BARRY E. & MICHAEL H. GRAYUM. Preliminary Report on the Flora Project of La Selva Field Station, Costa Rica 420

HUFT, MICHAEL. *Pseudocroton tinctorius* Muell. Arg., a Synonym of *Capparis indica* (L.) Fawc. & Rendle 426

HUMPHRIES, C. J. Vicariance Biogeography in Mesoamerica 444

KEATING, RICHARD C. The Evolution and Systematics of Onagraceae: Leaf Anatomy 770

KENTON, ANN (See Ching-I Peng & Ann Kenton) 418

KRAL, ROBERT & LYMAN B. SMITH. *Xyris apureana* Kral & Smith, A New Species of *Xyris* (Sect. *Nematopis*) from Venezuela 412

KRAL, ROBERT. *Xyris nigrescens* Kral, a New Species of *Xyris* (Sect. *Nematopus*) from Costa Rica 415

MCDADE, LUCINDA A. Three New Species of *Aphelandra* (Acanthaceae) from Central America 402

MCLAUGHLIN, STEVEN P. A Revision of the Southwestern Species of *Amsonia* (Apocynaceae) 336

MARTIN, HELENE A. Changing Cenozoic Barriers and the Australian Paleobotanical Record 625

MOHLENBROCK, ROBERT H. Illinois Convolvulaceae in the Missouri Botanical Garden Herbarium 393

MOHLENBROCK, ROBERT H. Illinois Solanaceae in the Missouri Botanical Garden Herbarium and Biographical Sketches of Some Collectors 382

MORIN, NANCY R. Biological Studies in Central America: The Twenty-Eighth Annual Systematics Symposium 431

PENG, CHING-I & ANN KENTON. Chromosome Number of *Byblis liniflora* Salisb. (Byblidaceae) 418

PRANCE, GHILLEAN T. A Review of the Phytogeographic Evidences for Pleistocene Climate Changes in the Neotropics 594

RAVEN, PETER H. (See Dennis E. Breedlove, Paul E. Berry & Peter H. Raven) 209

RAVEN, PETER H. Nomenclatural Corrections in the Genus *Camissonia* (Onagraceae) 995

ROBBRECHT, ELMAR. The Identity of the Panamanian Genus *Dressleriopsis* (Rubiaceae) 427

RUNDEL, PHILLIP (See Peter R. Atsatt & Phillip Rundel) 199

SAVAGE, JAY M. The Enigma of the Central American Herpetofauna: Dispersals or Vicariance? 464

SMITH, LYMAN B. (See Robert Kral & Lyman B. Smith) 412

SOLOMON, JAMES C. The Systematics and Evolution of *Epilobium* (Onagraceae) in South America 239

TAGGART, RALPH E. (See Aureal T. Cross & Ralph E. Taggart) 676

WHITMORE, T. C. Wallace's Line: A Result of Plate Tectonics 668

ANNALS
OF THE
MISSOURI BOTANICAL GARDEN

VOLUME 69 1982 NUMBER

FUCHSIA NIGRICANS LINDE

STUDIES IN *FUCHSIA*

CONTENTS

The Systematics and Evolution of *Fuchsia* Sect. *Fuchsia* (Onagraceae) *Paul E. Berry* 1

Pollinator Maintenance vs. Fruit Production: Partitioned Reproductive Effort in Subdioecious *Fuchsia lycioides* *Peter R. Atsatt & Phillip Rundel* 199

The Mexican and Central American Species of *Fuchsia* (Onagraceae) except for Sect. *Encliandra* *Dennis E. Breedlove, Paul E. Berry & Peter H. Raven* 209

The Dennis Stanfield Award 234

The 1982 Jesse M. Greenman Award 234

Index 235

Additional copies of this special issue are available from the Missouri Botanical Garden.
See page 1 for ordering information.

VOLUME 69
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THE SYSTEMATICS AND EVOLUTION OF *FUCHSIA* SECT. *FUCHSIA* (ONAGRACEAE)[1]

PAUL E. BERRY[2]

ABSTRACT

Nine sections are currently recognized in the genus *Fuchsia*, consisting of approximately 100 species. Morphological and biogeographical evidence indicates a Paleogene origin of the genus in temperate South America, with two early lines diverging to New Zealand and North America. Within South America, sects. *Quelusia* and *Kierschlegeria* have remained in the southern part of the continent, while the two largest sections, *Fuchsia* and *Hemsleyella*, have developed in the tropical Andes.

[1] Copies of this special issue of the Annals of the Missouri Botanical Garden can be obtained by sending $7.50 per copy to Department Eleven *Studies in Fuchsia*, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166. This material is based upon research supported by the National Science Foundation under Grants No. DEB 78-05969 (to P.B.) and DEB 78-23400 (to Peter H. Raven) and is published with support of National Science Foundation Grant No. DEB-8122087. The Foundation provides awards for research and education in the sciences. The awardee is wholly responsible for the conduct of such research and preparation of the results for the publication. The Foundation, therefore, does not assume responsibility for such findings or their interpretation. Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the author and do not necessarily reflect the views of the National Science Foundation. A grant-in-aid from Sigma Xi helped to support the initial stages of the field work. The color illustrations and some of the figures were prepared by the Unidad de Medios Audiovisuales, Universidad Simón Bolívar, Caracas, Venezuela. The Universidad Simón Bolívar also generously covered the costs of the color plates, through the Decanato de Investigaciones. This support is gratefully acknowledged.

This study was undertaken as part of my doctoral thesis studies at Washington University, St. Louis, Missouri. I am especially thankful to Dr. Peter H. Raven for his continual interest, encouragement, and support throughout the realization of this study. The assistance of the staff and technicians of the Missouri Botanical Garden greatly facilitated my work and is strongly appreciated. I extend special thanks to Dr. Stephen S. Tillett (Herbario Ovalles, Facultad de Farmacia, Universidad Central de Venezuela) for providing advice and laboratory facilities during extended stays in Caracas, to Dr. Julian A. Steyermark (Instituto Botánico, Caracas) for his ongoing help and encouragement, and to Dr. Peter Hoch (Missouri Botanical Garden) for carefully reviewing the final draft of my thesis. My companions W. Wagner, T. P. Ramamoorthy, and J. Solomon provided helpful discussion and assistance in the preparation of this paper. The illustrations were expertly done by Eduardo Pérez; Gabriela Aedo assisted with maps and diagrams.

Many persons generously gave of their time and knowledge to assist me in the field work. I would specifically like to mention the late Dr. Luís Ruiz-Terán (Mérida, Venezuela); also, Dr. César Vargas C. (Cuzco, Peru), Dr. Ramón Ferreyra (Museo de Historia Natural Javier Prado, Lima, Peru), Dr. Abundio Sagástegui (Universidad Nacional de Trujillo, Peru), Ingº Alberto Ortega (Universidad Nacional, Quito, Ecuador), Dr. Fernando Ortiz (Universidad Católica, Quito, Ecuador), Linda Albert de Escobar (Comisión Fulbright, Quito, Ecuador), Lic. Olga Benavides (Universidad de Nariño, Pasto, Colombia), Ingº Eugenio Escobar (Universidad del Valle, Palmira, Colombia), Dr. Luis Mar-

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This paper treats the systematics of *Fuchsia* sect. *Fuchsia,* which includes 61 species, ten of them newly described here. Despite the large number of species compared to other sections in the genus, sect. *Fuchsia* appears to be a natural grouping of species. These species all have morphological variations on a common theme, namely shrubs with tubular, reddish flowers pollinated mostly by hummingbirds. The main differences between species occur in the shape, length, or coloration of the floral tube and in the position of flowers in the leaf axils or in different kinds of racemose inflorescences.

The close relationship between species in sect. *Fuchsia* is indicated by their high level of interfertility with numerous naturally occurring hybrids and by chromosome numbers that are invariate or on just two levels. From over 100 new chromosome counts in populations of sect. *Fuchsia,* 37 species are now known as diploids ($n = 11$), five as tetraploids, and one species has both diploid and tetraploid populations. Chromosomal pairing in interspecific hybrids was normal in all cases examined. Naturally occurring interspecific hybrids were found in 17 different combinations, and, in two instances, populations of probable hybrid origin appear to be more successful than their local parental populations.

Altitudinal stratification of species along mountain slopes is a major isolating mechanism between different species of sect. *Fuchsia*. Though sympatry is common, species that differ substantially in floral tube length and coloration may diminish or prevent interspecific pollination by hummingbirds. Sect. *Fuchsia* possesses a particularly flexible reproductive system, combining limited vegetative reproduction with a long, essentially aseasonal flowering period in which modal outcrossing is prevalent, but autogamy also occurs.

The cool, montane habitats of the Andes presently occupied by sect. *Fuchsia* have arisen largely in the Neogene. The Andean chain actually is composed of a number of distinct structural units, each one differing somewhat in its orogeny and floristic/faunistic composition. Distributional patterns of species in the different structural units suggest that sect. *Fuchsia* has undergone a recent differentiation closely tied to the major elevation of the Andes in the Pliocene and to the glacial events and climatic fluctuations that took place during the Pleistocene. The recent diversification of most species in the section is further supported by the morphological and cytological similarities noted above, as well as by the large numbers of species in the Andes compared to other areas where *Fuchsia* occurs, and the small geographic ranges of most species there. The ability to hybridize and recombine genetic material, the presence of self-compatibility allowing establishment from a single seed after dispersal, and the recent uplift and climatic fluctuations of the Andes have probably been the key factors in the differentiation of species in *Fuchsia* sect. *Fuchsia*.

Fuchsia is a large, distinctive genus that lacks close affinities with any other group in the Onagraceae and therefore is classified as a monogeneric tribe. Its approximately 100 species are mostly mesophytic shrubs that grow in the Andes from Colombia and Venezuela to Tierra del Fuego, the southeastern coastal mountains of Brazil, Hispaniola, and the mountains of Mexico and Central America, with a small disjunct section in New Zealand and Tahiti. On the basis of chromosome number and morphology (Kurabayashi et al., 1962), floral anatomy (Eyde & Morgan, 1973), wood anatomy (Carlquist, 1975), and leaf architecture (Hickey, 1980), *Fuchsia* appears to be one of the least specialized genera in the family. In its red, tubular, bird-pollinated flowers and fleshy, bird-dispersed fruits, however, *Fuchsia* as it exists today is clearly specialized. Both *Fuchsia* and *Ludwigia,* a genus that is also relatively unspecialized and represents a phylo-

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cano-Berti (Universidad de Los Andes, Mérida, Venezuela), and Dr. Gary L. Smith and Milcíades Mejía (Jardin Botánico Rafael Moscoso, Santo Domingo, Dominican Republic).

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Finally, my deep thanks go to my wife Eva and to Danny, who endured long separations so that this paper could be completed.

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genetic line distinct from the remainder of the family, have their center of distribution in South America, which may have been the center of origin for the family (Raven & Axelrod, 1974). In light of these relationships, an understanding of the evolutionary modes in *Fuchsia* will be fundamental to the overall understanding of evolution in the Onagraceae.

In the past 15 years, detailed systematic studies have been completed for a number of the small sections of the genus. Sect. *Encliandra* (six spp., Central America and Mexico) was revised by Breedlove (1969), sect. *Skinnera* (four spp., New Zealand and Tahiti) by E. Godley and P. H. Raven (unpublished), and finally sect. *Schufia* (two spp., Central America and Mexico) and the new sections *Ellobium* (three spp., Central America and Mexico) and *Jimenezia* (one sp., Costa Rica and Panama) by Breedlove et al. (1982). These sections, some of which present interesting developments such as male sterility and wide disjunctions in range, represent less than a fifth of the total number of species in the genus. The great majority of species of *Fuchsia* are concentrated in Andean South America, and about three-fifths of the total belong to the section treated here.

Fuchsia sect. *Fuchsia* was selected for the present revision because of its comparatively large size, with over 60 closely related species, and because it can be expected to provide a model of evolution widely applicable to other groups of the poorly studied tropical Andes. Emphasis was placed primarily on field examination of populations and morphological analysis of herbarium specimens from the major collections of the world. In this manner, the amount of hybridization and the principal isolation mechanisms operating between species could be evaluated along with morphological characters to determine more accurately species limits within the section. In addition, chromosome counts were obtained for 43 of the 61 species recognized in sect. *Fuchsia*. Concurrently with this study, an analysis of leaf flavonoids (J. Averett et al., in prep.) as well as a detailed, ultrastructural pollen survey of the entire genus (J. Nowicke et al., in prep.; J. Praglowski et al., in prep.) are nearing completion, and systematic studies are underway in the remaining three sections from South America, *Quelusia, Kierschlegeria* and *Hemsleyella* (P. E. Berry and T. P. Ramamoorthy, in prep.).

Origin of the Genus and Subgeneric Relationships

Age and Relationships of *Fuchsia*

Despite the unequivocal familial limits of the Onagraceae, no clear relationships are apparent between the seven tribes in the family. Although no tribe presents a series of features that can be considered ancestral to the rest, *Ludwigia*, the sole genus of the Jussiaeeae, is the most distinct and clearly represents an early offshoot of the family (Raven, 1979a). The other six tribes are therefore more closely related to one another than any one is to *Ludwigia*. The monogeneric tribe Fuchsieae is the tribe with the largest assemblage of unspecialized features, including the absence of interxylary phloem and unspecialized chromosomes and placentation (Eyde & Morgan, 1973).

The order Myrtales, to which the Onagraceae belong, is clearly a southern hemisphere group (Raven & Axelrod, 1974). *Ludwigia* has its least specialized

TABLE 1. Main historical subdivisions of *Fuchsia*.

Author	Equivalent Modern Sections[1]
DECANDOLLE (1828)	
Sect. *Quelusia*	
Breviflorae	*Encliandra, Kierschlegeria*
Macrostemonae	*Fuchsia* (part), *Quelusia, Schufia*
Longiflorae	*Fuchsia* (part), *Hemsleyella, Ellobium*
Sect. *Skinnera*	*Skinnera*
ENDLICHER (1840)	
a. *Encliandra*[2]	
Brebissonia	*Encliandra* (part)
Lyciopsis	*Encliandra* (part)
b. *Fuchsia*[2]	
Kierschlegeria	*Kierschlegeria*
Fuchsia	*Fuchsia, Quelusia*
Schufia	*Schufia*
c. *Skinnera*[2]	*Skinnera*
HEMSLEY (1877)	
"American species having petals"	
Tropical Andean species	*Fuchsia*
Brazilian species	*Quelusia* (part)
South Andean species	*Quelusia* (part), *Kierschlegeria*
Mexican and Central American species	*Encliandra, Schufia, Ellobium*
"American species destitute of petals"	*Hemsleyella*
"New Zealand species"	*Skinnera*
MUNZ (1943)	
Sect. *Quelusia*	*Quelusia*
Sect. *Fuchsia*	*Fuchsia, Ellobium* (part)
Sect. *Kierschlegeria*	*Kierschlegeria*
Sect. *Skinnera*	*Skinnera*
Sect. *Hemsleyella*	*Hemsleyella, Ellobium* (part)
Sect. *Schufia*	*Schufia*
Sect. *Encliandra*	*Encliandra*

[1] Includes only groups or species known at the time of publication.
[2] Groups of undesignated rank, but subsequently taken up as sections by Walpers (1843), Bentham & Hooker (1867), and Baillon (1877).

members and greatest species diversity in South America, as well as all of its self-incompatible species. *Fuchsia* likewise has by far its greatest concentration of species in South America and had reached New Zealand by the latest Oligocene (Mildenhall, 1980). Because of these relationships, it has been hypothesized that the Onagraceae originated in South America (Raven & Axelrod, 1974; Raven, 1979a). All of the remaining tribes of the family, however, have their centers of diversity in the northern hemisphere, and fossil pollen of *Ludwigia* is known from the northern hemisphere from the early Paleogene onward (Eyde & Morgan, 1973). Thus very early dispersal between the two hemispheres clearly occurred. The Onagraceae originated by the close of the Cretaceous (Raven & Axelrod, 1974); earliest fossil remains assignable to genera are from the Paleocene for *Ludwigia* and the Oligocene for *Circaea*. The earliest fossil record for *Fuchsia*

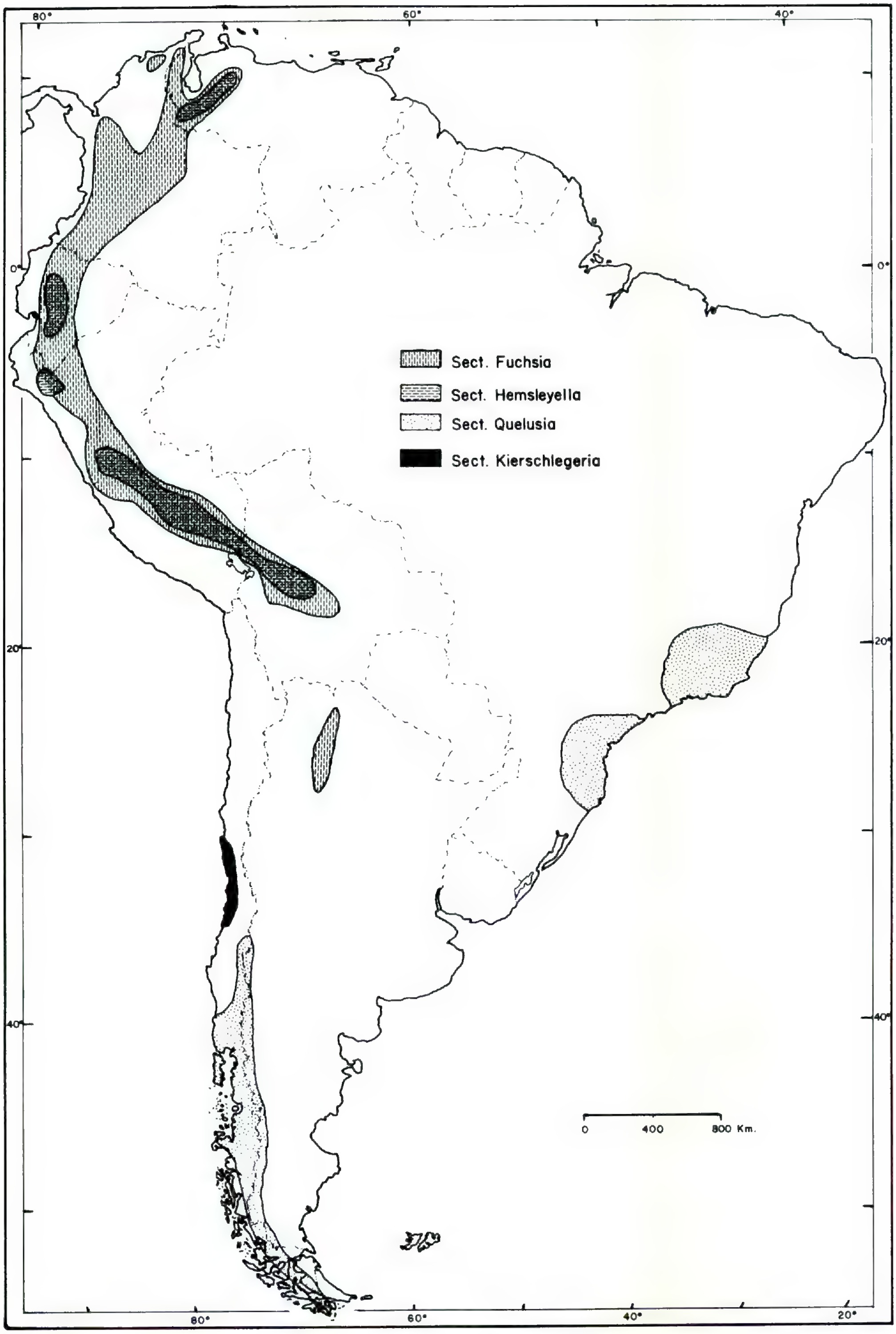


FIGURE 1. Native distributions of the South American sections of *Fuchsia*.

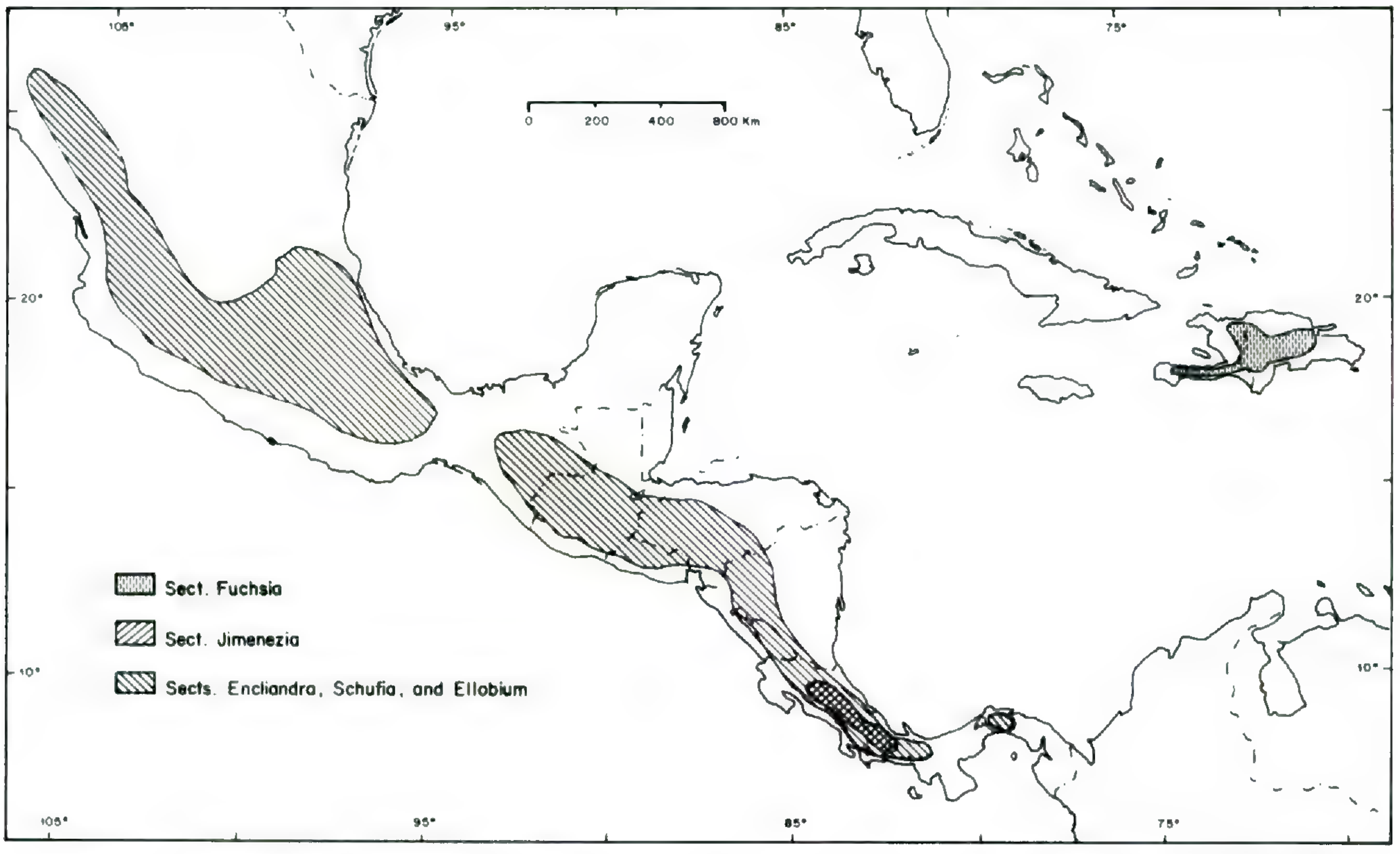


FIGURE 2. Native distributions of the sections of *Fuchsia* outside of South America, not including sect. *Skinnera*, which is endemic to New Zealand and Tahiti.

is pollen from the uppermost Oligocene of New Zealand (Couper, 1960; Mildenhall, 1980), which gives us a minimum age for the genus. Because of the possession of a number of advanced characters, the New Zealand species of *Fuchsia* are almost certainly derived from American ancestors, so the genus probably evolved considerably earlier. Bird pollination is a dominant theme in *Fuchsia* and is present in both New World and Old World groups; the fruits are also adapted to bird dispersal. Specialized flower-visiting birds probably did not evolve until the Eocene (Sussman & Raven, 1978), but it is uncertain whether the common ancestor of *Fuchsia* would have been bird-pollinated or not. At any event, plants similar to the existing species of *Fuchsia* probably could not have evolved prior to the Eocene. The most likely hypothesis, therefore, is that the genus originated in the Eocene or Oligocene in South America.

SUBGENERIC TREATMENTS OF *FUCHSIA*

Attempts to recognize several related genera in the tribe Fuchsieae, such as Spach's (1835) treatment, have met with little acceptance because of the existence of intermediate taxa linking the most divergent species and because of the lack of fundamental differences in the basic features of the group. In contrast, a number of infrageneric groups have traditionally been recognized as sections or as groups of undesignated rank. A synopsis of the different subgeneric treatments of *Fuchsia* until Munz's (1943) generic monograph is listed in Table 1.

DeCandolle (1828) divided the genus into sect. *Skinnera*, from New Zealand, and sect. *Quelusia*, from America. He based his subdivisions of sect. *Quelusia* on the degree of staminal exsertion and the relative length of the floral tube and

TABLE 2. The sections of *Fuchsia* and their native geographical distribution.

Section	Estimated number of Species	Distribution
1. *Quelusia*	5	SE coastal Brazil, Chile & Argentina
2. *Fuchsia*	61	Tropical Andes, Hispaniola
3. *Ellobium*	3	Mexico and Central America
4. *Hemsleyella*	14	Tropical Andes
5. *Kierschlegeria*	1	Central coastal Chile
6. *Schufia*	2	Mexico and Central America
7. *Jimenezia*	1	Panama and Costa Rica
8. *Encliandra*	6	Mexico and Central America
9. *Skinnera*	4	New Zealand and Tahiti
TOTAL:	97	

sepals. His subdivisions represent what now seems to have been an unnatural division of the presently recognized sections. Endlicher (1840) made a few improvements over DeCandolle's treatment, such as the segregation of the distinctive *Schufia* group and the separation of *Kierschlegeria* from *Encliandra*. Despite Hemsley's (1877) informal style of presentation, his arrangement is remarkably close to our modern sectional concepts of the genus. Through his geographical criteria and familiarity with living, introduced species, Hemsley first recognized the integrity of the modern sects. *Fuchsia*, *Hemsleyella*, and, in part, *Quelusia*. Finally, Munz's (1943) generic revision ordered the previous diverse subgeneric concepts into a consistent, formal system consisting of seven sections.

Recent study of the Mexican and Central American species of *Fuchsia* has introduced several changes into Munz's sectional classification (Breedlove et al., 1982). The currently recognized sections are listed along with their native distribution and species numbers in Table 2, and maps of their distributions appear in Figures 1 and 2.

KEY TO THE SECTIONS OF *FUCHSIA*

1a. Petals lacking or much reduced, if present, less than one third the length of the sepals and with floral tubes 5–15 mm long; leaves generally alternate.
  2a. Floral tube 5–15 mm long; gynodioecious or dioecious; leaves usually present when flowering; New Zealand and Tahiti. ---------- sect. *Skinnera*
  2b. Floral tube 17–170 mm long; hermaphroditic; often flowering when leafless; South America. ---------- sect. *Hemsleyella*
1b. Petals present, usually conspicuous and more than one third the length of the sepals, if shorter, with floral tubes 20–130 mm long; leaves generally opposite or whorled.
  3a. Antepetalous stamens reflexed and included in the floral tube.
    4a. Flowers axillary, dioecious or subdioecious; berries with 6–35 seeds; Mexico to Panama. ---------- sect. *Encliandra*
    4b. Flowers in terminal racemes or panicles, hermaphroditic; berries with 35–80 seeds; Costa Rica and Panama. ---------- sect. *Jimenezia*
  3b. Stamens all erect and exserted beyond the floral tube.
    5a. Small trees; flowers numerous, erect in well-developed di- or trichotomously branched panicles. ---------- sect. *Schufia*
    5b. Shrubs, climbers, or epiphytes, rarely arborescent; flowers spreading or pendant and axillary, racemose, or in few-branched panicles.
      6a. Petiole bases persisting as woody, spinose knobs on the stem; subdioecious; floral tube 3–10 mm long and sepals reflexed; berries with 14–30 seeds. ---------- sect. *Kierschlegeria*

6b. Petioles dehiscing flush with the stem and never spinose; hermaphroditic; floral tube 10–130 mm long or, if shorter, sepals not reflexed; berries with 30–250 seeds.
  7a. Floral tubes usually shorter than the sepals, these ± connate at the base; stamens exserted well beyond the sepals; petals convolute after anthesis; flowers axillary; Southern Andes and southeast Brazil (introduced elsewhere). ---------- sect. *Quelusia*
  7b. Floral tubes usually longer than the sepals, if not, with sepals free to the base; stamens generally not exserted beyond the sepals, petals not overlapping at anthesis; flowers axillary, racemose, involucrate, or paniculate; Central Andes to Mexico and Hispaniola.
    8a. Leaves mostly opposite, broad, elliptic-ovate or cordate; tubers present, or plants epiphytic, if not, with green petals; nectary a smooth, unlobed band lining the base of the tube; Central America and Mexico. ---------- sect. *Ellobium*
    8b. Leaves opposite to whorled, variously shaped but generally not cordate at the base; tubers lacking; plants terrestrial, the petals never green; nectary annular and mostly free from the base of the tube or with prominent lobes adnate to it; South America and Hispaniola (introduced elsewhere). ---------- sect. *Fuchsia*

INTERSECTIONAL RELATIONSHIPS AND EVOLUTIONARY LINES IN *FUCHSIA*

As discussed previously, *Fuchsia* probably originated in South America. The genus almost invariably occurs in cool, mesic climates and is centered in tropical uplands or temperate forest below the frost zone. The three main ecogeographic areas of South America occupied by *Fuchsia* are 1) cloud forests of the tropical Andes, 2) *Nothofagus* forest in the temperate Andes, and 3) montane forest in southeastern Brazil. The floristic relationships of these three areas have been pointed out by numerous authors, including Gerth (1941), Smith (1962), and Vuilleumier (1969), based on such diverse taxa as *Araucaria*, *Drimys*, *Berberis*, *Lepechinia*, *Podocarpus*, *Ilex*, *Chusquea*, and *Perezia*. These elements are considered to be remnants of ancient, widely distributed temperate forests across southern South America (Simpson, 1973, 1979). Paleontological, paleoclimatic, and geological evidence indicates that a generally warm and equable climate prevailed throughout South America in the early Tertiary, with tropical rainforest vegetation extending considerably farther south than at present (see reviews in Vuilleumier, 1969; Simpson 1973, 1979; Haffer, 1974; Solbrig, 1976; Duellman, 1979). Fossil evidence of fully tropical wet forest is known from the Eocene in Argentina at 38°S, with subtropical woods and pampa occurring at 42°S. A marked cooling and drying trend began in the Oligocene and Miocene, however, with the result that temperate elements of the Antarcto-Tertiary Geoflora migrated farther north, replacing the tropical flora of Chile and Argentina. In the Oligocene, austral forests of *Nothofagus*, *Araucaria*, and *Laurelia* were present as far north as 30°S in Argentina (Jeannel, 1967). Subsequently the continuity of this continuous forest was broken up by the rain shadows created by the rising Andes and by the spread of the Tertiary-Chaco Geoflora (Solbrig, 1976). The fragmentation of the once widespread southern forests continued, and by the Pliocene most of the *Nothofagus* forests east of the Andes had disappeared completely.

Given this background, we may hypothesize that the ancestral stock of *Fuchsia* evolved within the southern temperate forests of South America during the Eocene or Oligocene. Several main lines of the genus probably diverged in the

late Oligocene and Miocene, when the austral forests began to contract and fragment, and the Andes began to be uplifted substantially. One of the earliest offshoots of *Fuchsia* was sect. *Skinnera*. As indicated by pollen fossils (Mildenhall, 1980), *Fuchsia* was present in New Zealand, where there are three very distinct species of sect. *Skinnera*, by the late Oligocene. It probably spread across Antarctica, contrary to the earlier view of Raven, who postulated a long distance dispersal route across the Pacific (Raven, 1972a, p. 242). At that time, *Fuchsia* had not been reported from New Zealand prior to the middle Miocene, and it was not understood that more or less direct opportunities for migration across Antarctica persisted until the Miocene (Raven, 1979b). The fourth species of sect. *Skinnera*, *F. cyrtandroides*, is endemic to the Pacific island of Tahiti, which is of volcanic origin and less than two million years old (Dymond, 1975). This species undoubtedly arrived there from New Zealand by long distance bird transport, since the entire Tahitian flora is adapted to long distance dispersal, and nearly 40% of the plant species there are adapted to internal transport by birds (Carlquist, 1967). Members of sect. *Skinnera* are probably better adapted to long distance transport than are other sections of the genus because they have the smallest and most numerous seeds (up to 450 per fruit) in the genus.

Other distinctive characters reflect the early divergence of sect. *Skinnera*. Initial results of a survey of leaf flavonoids in the genus indicate that it is the only section with what appears to be sulfated flavonoids (J. Averett et al., in prep.). It also includes the most widely divergent growth forms in the genus—procumbent creepers, lianas, and tall trees. A strong reduction of petals occurs in the section, and it has smooth, band-type nectaries like those of sects. *Hemsleyella* and *Ellobium* and beaded viscin threads on the pollen as in all South American sections except sect. *Kierschlegeria*.

Another offshoot probably spread early in the history of the genus to North America by long distance dispersal, most likely in Paleogene time. Other families that show this pattern of an early South to North American migration include Cactaceae, Loasaceae, Nyctaginaceae, and Zygophyllaceae (see Raven & Axelrod, 1974, pp. 627 and 628 for more complete lists). This early offshoot of *Fuchsia* that reached North America eventually differentiated into the modern sects. *Encliandra*, *Jimenezia*, and *Schufia*. Though each one of these sections is now quite distinct from each other, common ancestry is suggested by the following shared characters: smooth viscin pollen threads (though a few intermediate types occur in sect. *Encliandra*), small flowers adapted to insect pollination in several species, and similar lobed-adnate nectaries. Other derived characters are the presence of male sterility in sects. *Encliandra* and *Schufia*, antepetalous stamens reflexed into the floral tube in sects. *Encliandra* and *Jimenezia*, and low seed or ovule number in sect. *Encliandra*. Sections *Encliandra* and *Schufia* have their center of diversity in Mexico and only secondarily spread south of the Isthmus of Tehuantepec (Breedlove, 1969; Breedlove et al., 1982). Section *Jimenezia*, clearly closely related to, but more primitive than, sect. *Encliandra*, is monotypic and endemic to a small area of Costa Rica and Panama.

The remaining sections represent the majority of the species in the genus; they probably arose from a common ancestor as the austral temperate forests of South America became increasingly limited in area and the Andes were uplifted

during the Miocene and Pliocene. Sections *Quelusia, Fuchsia, Hemsleyella,* and *Ellobium* are all basically hummingbird-pollinated, hermaphroditic, and have similar beaded viscin pollen threads. They differ in characters such as nectary type, petal size, ploidy level, pollen pore number, and habit, however. Because sect. *Quelusia* inhabits areas in southeastern Brazil and Chile-Argentina that are more directly related to the ancient austral temperate forests than are the areas of the remaining sections, we may infer that its relatively short floral tubes and exserted stamens are more primitive characters than the long tubes characteristic of the other sections. Simpson (1973) presented extensive biogeographical evidence that the present day South American *Nothofagus* forests are refuges for many taxa that may have been present and have changed little since the early to mid-Tertiary. Section *Quelusia* is entirely polyploid and may have retained certain primitive characters for this reason. As Simpson pointed out for other taxa, relatively little differentiation seems to have occurred in the *Nothofagus* forests compared to related species elsewhere. A single widespread species of *Fuchsia, F. magellanica,* is found in these forests today. In contrast, the remaining species of sect. *Quelusia* in southeastern Brazil have radiated strongly there, as have many other plant groups (see Smith, 1962, and Plowman, 1979, for examples).

Section *Kierschlegeria* consists of a single species, *Fuchsia lycioides,* that grows in the summer-dry coastal vegetation of central Chile. This is the only species in the genus that occupies a seasonally dry habitat, and it has evolved a series of xeromorphic adaptations such as small, deciduous leaves, spinose leaf bases, and thick seed coats. The habitats where it occurs did not exist before the Pleistocene, when the Andes reached their present elevation and the cold Humboldt Current brought on greatly increased aridity to the Pacific coast of south-central South America (Raven, 1973; Simpson, 1975a; Solbrig, 1976). Notwithstanding this, it probably began to evolve its peculiar constellation of characters earlier in local pockets of aridity at the margins of the tropics. The lobed-adnate nectaries, triporate pollen grains, and tetraploidy make a common origin with sect. *Quelusia* seem likely, especially in view of the geographical proximity of these groups. *Fuchsia lycioides* is dioecious (Atsatt & Rundel, 1982) and its low ovule number and conceivably even its smooth viscin threads might be specializations related to this aspect of its breeding system. It seems possible that the three-pored pollen characteristic of these sections and present in all genera of Onagraceae other than *Fuchsia,* might be a shared primitive characteristic of sects. *Quelusia* and *Kierschlegeria,* and not directly related to their polyploid nature.

Sections *Fuchsia* and *Hemsleyella* are sympatric and restricted to the moist slopes of the tropical Andes, except for two disjunct species of sect. *Fuchsia* on Hispaniola, in the West Indies. The ancestors of these two sections probably migrated northward from the austral temperate forests in South America into new, cool, montane habitats that began to develop on the eastern slopes of the central Andes as they began to rise during the Miocene. Large areas of cool Andean forest probably did not exist until the Pliocene, however, when the major uplift of the Andes occurred. Section *Fuchsia* occurs in aseasonal habitats and is petaloid and mostly diploid; most species have a particular annular nectary (see Figs. 42 and 43). Section *Hemsleyella,* in which polyploidy is more frequent, is apetalous and has evolved a series of seasonal adaptations linked to a predom-

inantly epiphytic habit. Members of this section usually live on rocks or trees that are subject to much higher water stress than plants of sect. *Fuchsia* that grow in moist soil nearby. Most species of sect. *Hemsleyella* have developed adaptations such as thick, tuberous stems and dry season flowering and leaf drop.

Section *Ellobium* was recently segregated from sects. *Fuchsia* and *Hemsleyella* and includes three species in Mexico and Central America (Breedlove et al., 1982). Despite its northern range, sect. *Ellobium* has clear South American affinities and is morphologically intermediate between sects. *Fuchsia* and *Hemsleyella,* having petals as in sect. *Fuchsia* and band nectaries as in sect. *Hemsleyella.* A clear specialization trend occurs in the section from a nontuberous, mostly aseasonal species with large petals to a strongly seasonal, tuberous, epiphytic, and nearly apetalous species. Unlike the sympatric sections *Schufia* and *Encliandra,* the most generalized species of sect. *Ellobium* occur from Costa Rica to Mexico, while the more specialized ones are restricted to Mexico. This distribution pattern and the probable young age of the related sects. *Fuchsia* and *Hemsleyella* indicates that sect. *Ellobium* reached Central and North America by an independent dispersal event from South America. Most likely, the ancestors of sect. *Ellobium* reached the high mountains of Costa Rica once the Pliocene land connection between North and South America was established, then differentiated farther north into seasonally drier habitats.

Summarizing, the most primitive existing sections of *Fuchsia* may be *Quelusia* and *Kierschlegeria,* of temperate habitats in southern South America. The ancestors of sect. *Skinnera* reached New Zealand from temperate South America prior to the close of the Oligocene. The common ancestor of the North American sections *Jimenezia, Encliandra,* and *Schufia* likewise may have been derived from antecedents that occurred in the Paleogene of temperate South America and reached similar habitats in North America. Generalized features for the genus may be sought by comparing characteristics common to these main groups. The differentiation of the more modern and related sections *Fuchsia, Hemsleyella,* and *Ellobium* in the Andes and, ultimately, North America, seems definitely to have been a Neogene phenomenon linked with the uplift of the Andes and the diversification of suitable habitats there, as well as with floral specialization to hummingbird pollination. The rest of this paper deals with the systematics and evolution of sect. *Fuchsia* and is aimed at analyzing how this particular line of the genus was able to differentiate so extensively in a relatively short time span. The patterns of evolution in this section should serve to illustrate comparable patterns in many other groups that inhabit the same areas, and that have been derived from diverse sources.

Ecology and Geographical Distribution

ECOLOGY

Habitat. Plants of *Fuchsia* sect. *Fuchsia* typically occupy moist, semidisturbed habitats of cool, montane forest. In the Andes this vegetation zone is commonly referred to as "cloud forest," but locally other terms are used such as "yungas" (Bolivia), "ceja" (Peru and Ecuador), and "montaña" (northern Andes). Lauer (1979) calls this formation the "tropical upper montane forest."

FIGURES 3–4. Habitats of *Fuchsia* sect. *Fuchsia* in the Andes.—3. Habitat of *F. venusta*, on the edge of a patch of cloud forest at 2,400 m in Dept. Tolima, Colombia. Arrow points to the position of flowering branches of *F. venusta*, found growing as a liana here. It also occurs as an erect or scandent shrub.—4. Habitat in which *F. venusta* (*Berry 3455*), *F. nigricans* (*Berry 3454*), and a hybrid between them (*Berry 3453*) were found growing together, between La Carbonera and La Azulita, 2,220 m, Edo. Mérida, Venezuela.

According to the Holdridge life zone system, the habitats of *Fuchsia* correspond to the humid, very humid, or pluvial montane or low montane life zones (Ewel et al., 1976). Three of Cuatrecasas' (1958) vegetation zones in Colombia are inhabited by *Fuchsia,* the upper part of the Subandean Forest (ca. 1,000–ca. 2,400 m), the Andean Forest (ca. 2,400–ca. 3,400 m), and the Subpáramo (ca. 3,400–ca. 4,000 m). Unlike the discontinuous and physiognomically distinct wet montane formations in much of Central America (oak–pine, mixed broadleaf forests), the cloud forests of the tropical Andes are essentially continuous on the eastern slopes from 12°N to 27°S latitude and are difficult to separate into distinct physiognomic units (Simpson, 1979).

The two main ecophysiological requirements of sect. *Fuchsia* are ample light and high, constant soil moisture. As shown by the long, wide vessel elements in the xylem and the lack of interxylary phloem (Carlquist, 1975), *Fuchsia* is clearly adapted to strongly mesic conditions. Because of their moderately high light requirements, plants of sect. *Fuchsia* are rarely found in tall or heavily shaded forests; the few plants that I have seen in such habitats were climbers that had reached the canopy or a light break in the forest (Fig. 3). Although seeds of *Fuchsia* germinate in the light, the inability of most species to withstand even moderate water stress prevents them from growing in open or strongly disturbed sites such as clearings or pastures. Many species of sect. *Fuchsia* are found growing in wet soil or near moving water, and they are typically found in thickets formed along road cuts or forest edges. In areas where human interference has

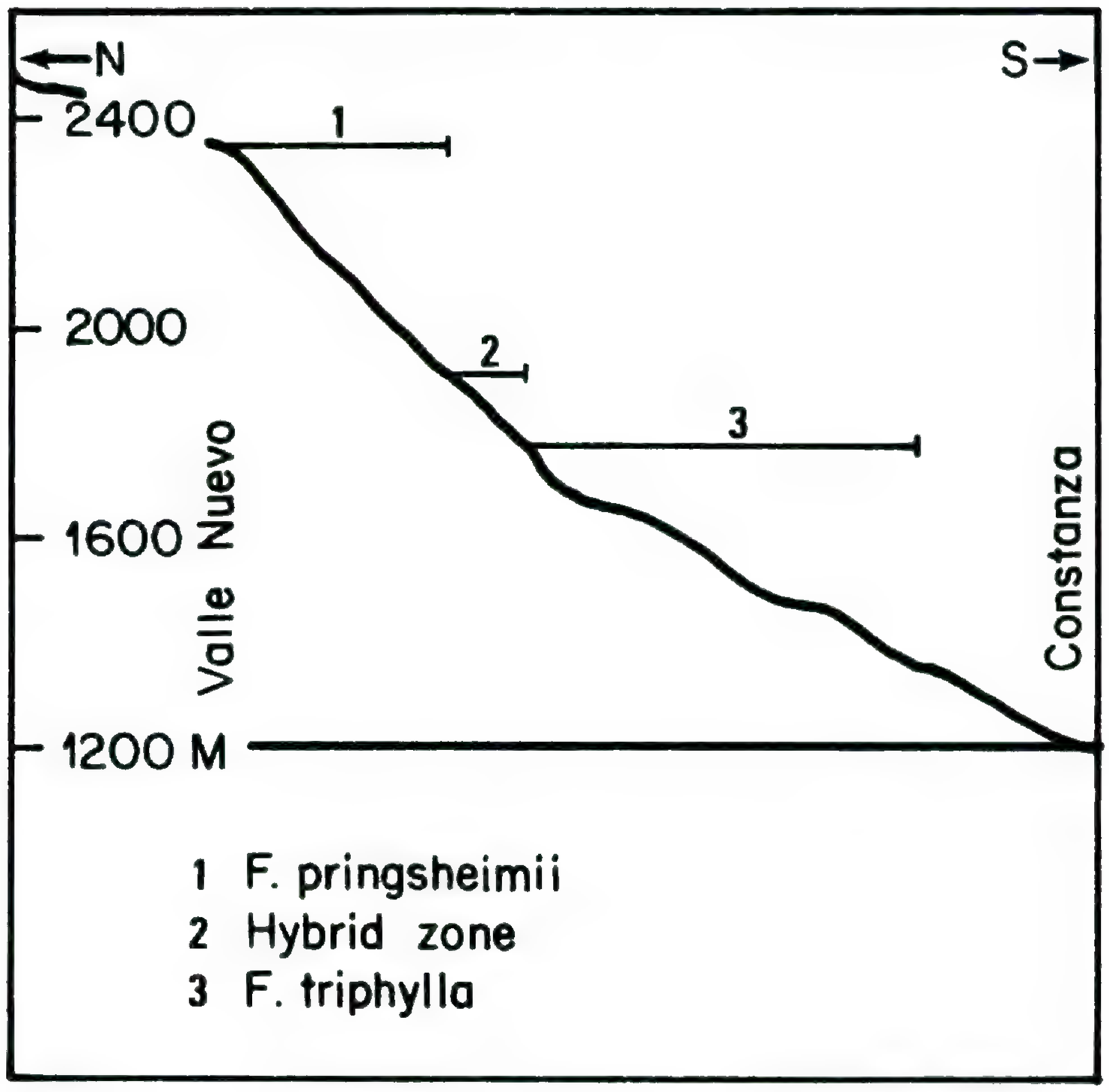


FIGURE 5. Altitudinal zonation of *Fuchsia* along a transect in Prov. La Vega, Dominican Republic.

been minimal, *Fuchsia* is found in naturally disturbed sites that can be fairly widespread on the steep slopes of wet forest, including treefalls, landslides, and streamsides. Larger populations are found in more open areas, however, so that a limited amount of human disturbance such as occasional clearings and road cuts seems to promote the growth and expansion of populations of most species in sect. *Fuchsia* (Fig. 4).

A few species occur outside of the cloud forest belt, either near its upper or lower limits or in drier formations. The *Fuchsia petiolaris* species group occurs at high elevations near the upper cloud forest limits and sometimes even extends into the páramo (Cleef, 1979). *Fuchsia vulcanica* is found at 4,000 m in northern Ecuador and southern Colombia, but *Fuchsia macrophylla* extends down into the subtropical forest at 1,200 m in central and southern Peru. *Fuchsia triphylla,* an endemic on Hispaniola, is exceptional in that it occasionally grows in open fields and also occurs as low as 1,000 m. Both *F. loxensis* and *F. dependens* are found in the high, rain-shadowed central valley of Ecuador, where they are usually found as mostly erect shrubs in hedgerows. *Fuchsia denticulata* is the only species in the section that inhabits the dry Pacific slopes of central Peru; it lives there in moist canyons mostly as an erect shrub, whereas the same species is a sprawling shrub or climber in cloud forests on the eastern slopes. The only widely naturalized species in the section, the arborescent *F. boliviana,* is tolerant of open habitats with moderate moisture stress, occupying a wider range of climatic conditions than most other species in the group.

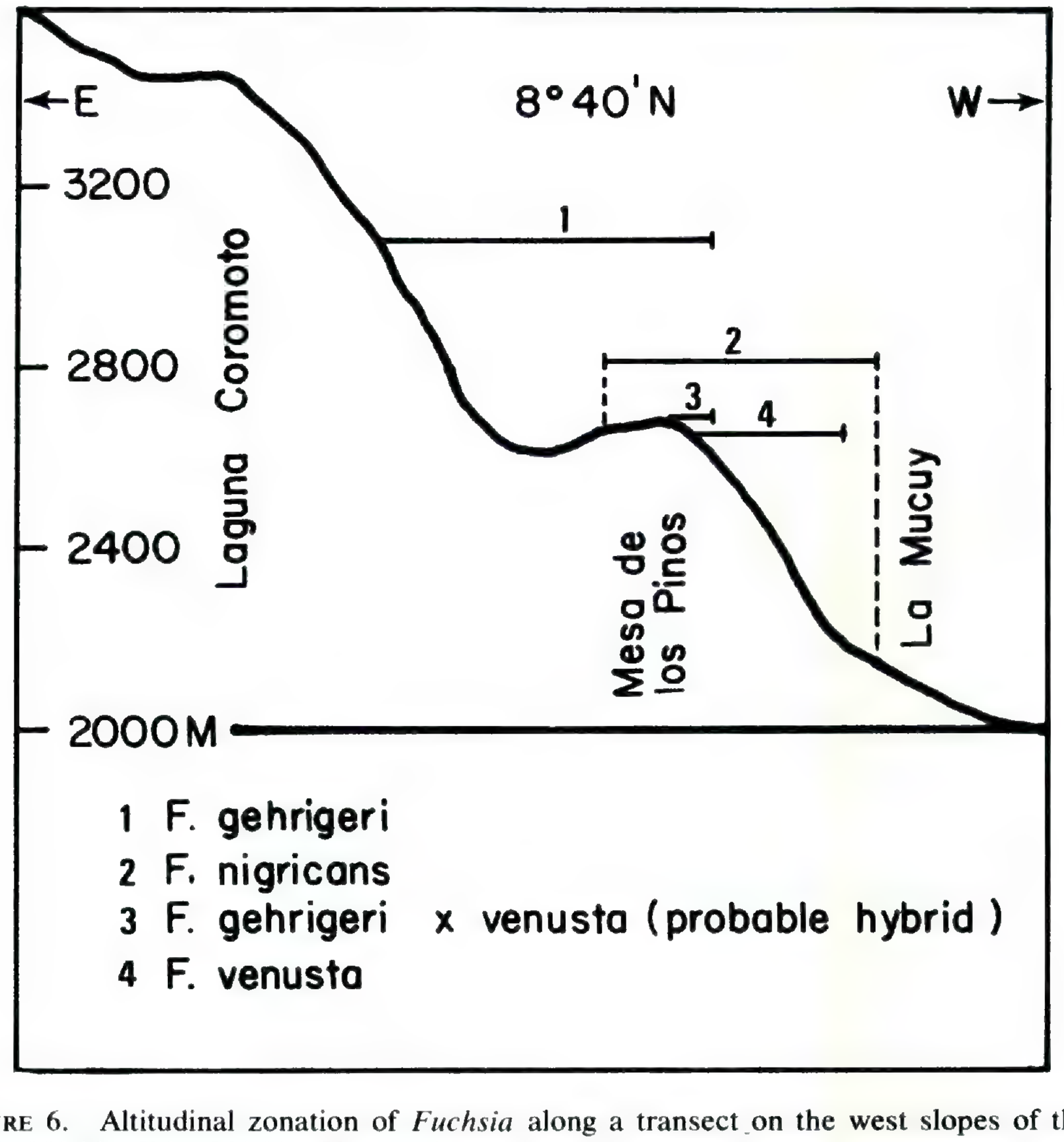


FIGURE 6. Altitudinal zonation of *Fuchsia* along a transect on the west slopes of the Sierra Nevada de Mérida, Edo. Mérida, Venezuela.

Altitudinal separation of species. Many species within sect. *Fuchsia* have different elevational tolerances, and the altitudinal stratification of species on the same mountain system is one of the principal isolating mechanisms operating between species. Hybrids are most often found where the altitudinal limits of partially sympatric species overlap. Figures 5 to 11 illustrate several examples of the successive altitudinal replacement of species on the same mountain range, which is found throughout the range of the section. The figures are based on data from field studies and herbarium specimens.

Phenology. Data from collection dates of herbarium specimens and field observations of populations of several species indicates that very little periodicity occurs in the flowering or appearance of new leaves in sect. *Fuchsia*. All the species are evergreen, and senescent leaves gradually fall off the older stems and are replaced by new leaves on the young axillary or terminal shoots. Individuals or local populations of *F. boliviana*, *F. dependens*, *F. nigricans*, and *F. venusta* are known to flower throughout the entire year.

Though annual temperature variation in the Andean cloud forests is slight, especially compared to the daily fluctuations, precipitation is seasonal, with one

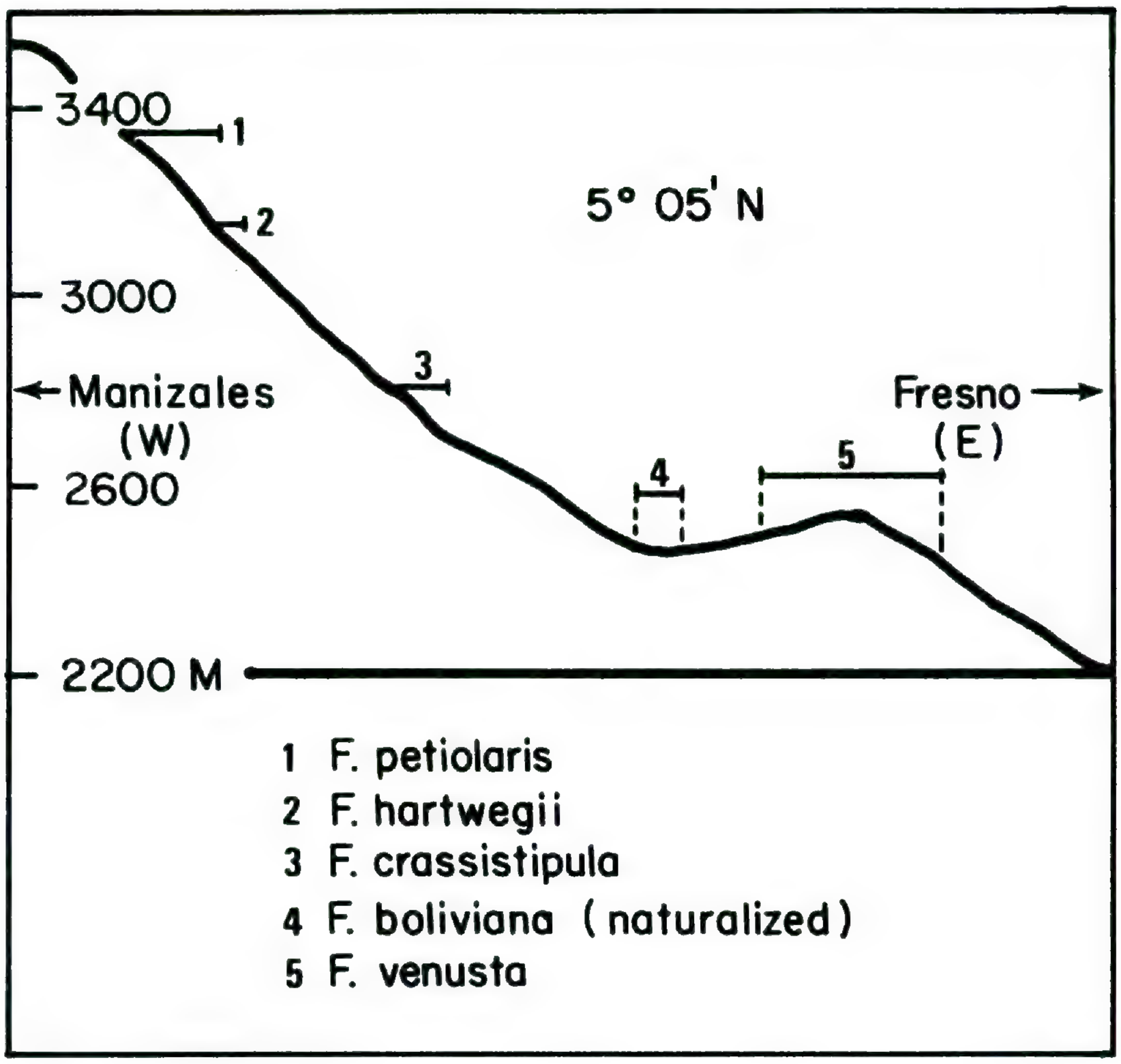


FIGURE 7. Altitudinal zonation of *Fuchsia* along a transect on the east slopes of the Cordillera Central in Dept. Tolima, Colombia.

or two relative dry seasons in different latitudes (Simpson, 1979). Definite growth cycles and periodicity in leaf and flower production occur in the sympatric sect. *Hemsleyella*. These plants, however, are mostly epiphytic or grow on rocks, where they are subject to much greater water stress, especially in drier periods. Members of sect. *Fuchsia* rarely experience a water deficit because they are terrestrial and grow in semi-shaded sites with high year-round soil moisture.

Section *Fuchsia* employs a "steady-state" flowering strategy (Gentry, 1974), whereby relatively few flowers are produced over an extended time period (usually a month or two). This strategy is adapted to pollinators with fixed foraging patterns such as bees and hummingbirds. It is important to note, however, that although pollination efficiency may be heightened by this strategy, temporal separation of flowering periods can *not* be an operative reproductive isolation mechanism in sect. *Fuchsia*.

GEOGRAPHICAL DISTRIBUTION

Geological background of the Andes. The Andes are a classic example of a mountain range that has a volcano-plutonic origin along a convergent plate margin (Sillitoe, 1974). As outlined in recent reviews of the Andean orogeny (Hammen, 1974; Haffer, 1974; Sillitoe, 1974; Simpson, 1975b, 1979; Flenley, 1979) three events in the history of the Andes have been of key importance to the develop-

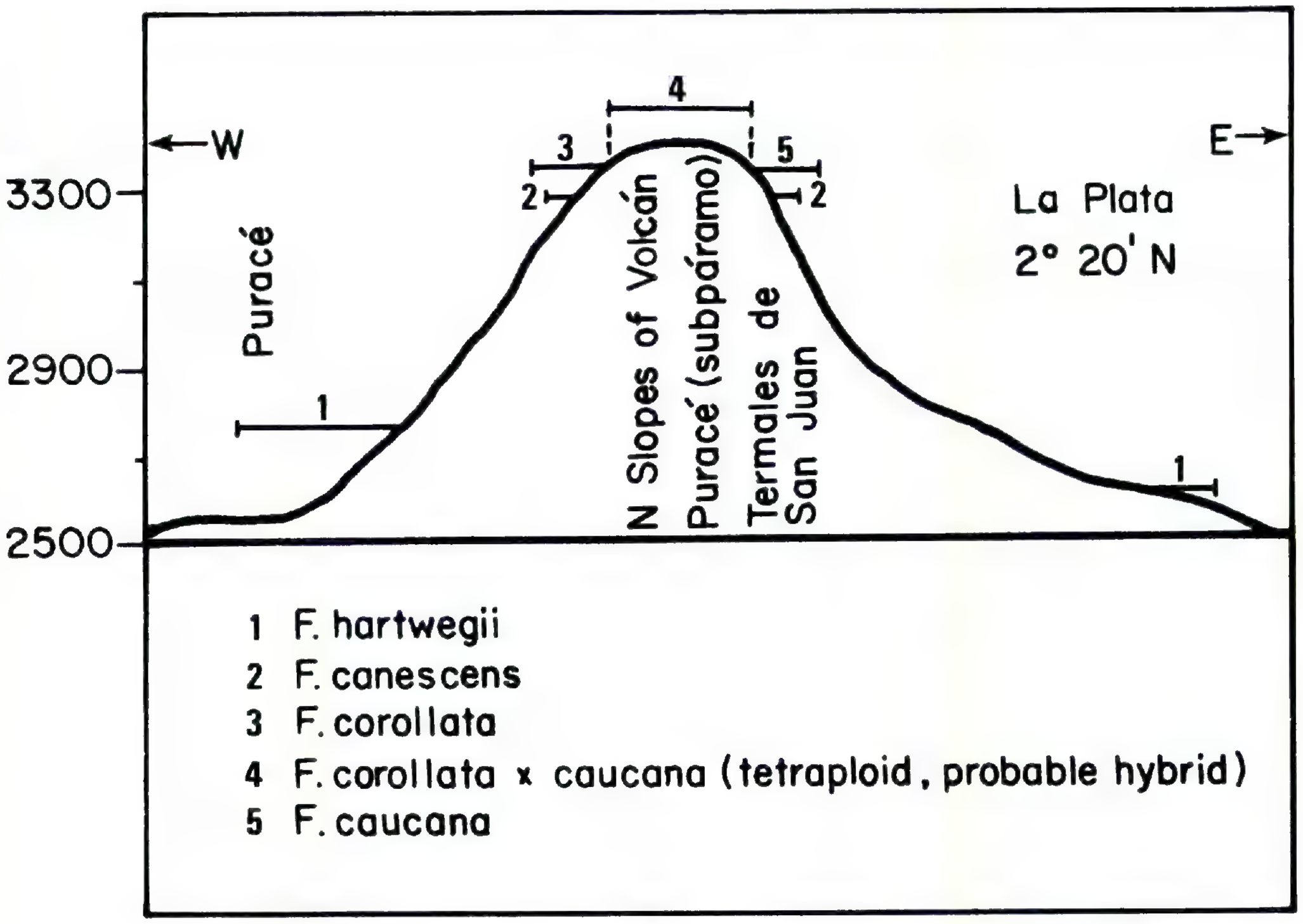


FIGURE 8. Altitudinal zonation of *Fuchsia* along a transect crossing the Cordillera Central in Depts. Cauca and Huila, Colombia.

ment of the native flora there. First, the final and major uplift throughout the Andes, accounting for an average 2,000–3,000 m increase in elevation, occurred toward the end of the Pliocene. As Hammen (1979) states, this implies that, at least in the northern Andes, the history of the Andean forest vegetation zone dates from the upper Miocene or lower Pliocene, while the páramo flora can only be traced back to the mid- to upper Pliocene. The youth of the high Andean flora is further demonstrated by the absence of endemic plant families in the páramos and by the low number of endemic páramo genera (Cleef, 1979).

Second, geomorphological and tectonic evidence indicates that, rather than having a longitudinally continuous orogeny, the Andes are actually composed of a number of separate, longitudinal segments (Fig. 12). The boundaries between these segments usually coincide with major changes in overall geology, strike, or even width of the Andes, and each segment represents a different piece of lithosphere that was individually subducted at probably different rates. The particular history of each segment affected its faunistic and floristic composition, and analyses such as those of Simpson (1975b) and Duellman (1979) have shown that distributions of Andean forest species tend to coincide with the basic geological discontinuities between structural units.

Finally, the Andes, as well as lowland tropical South America, were strongly affected during the Pleistocene by the same glacial cycles that drastically altered the climates of the temperate regions of the world. One to four major glaciations

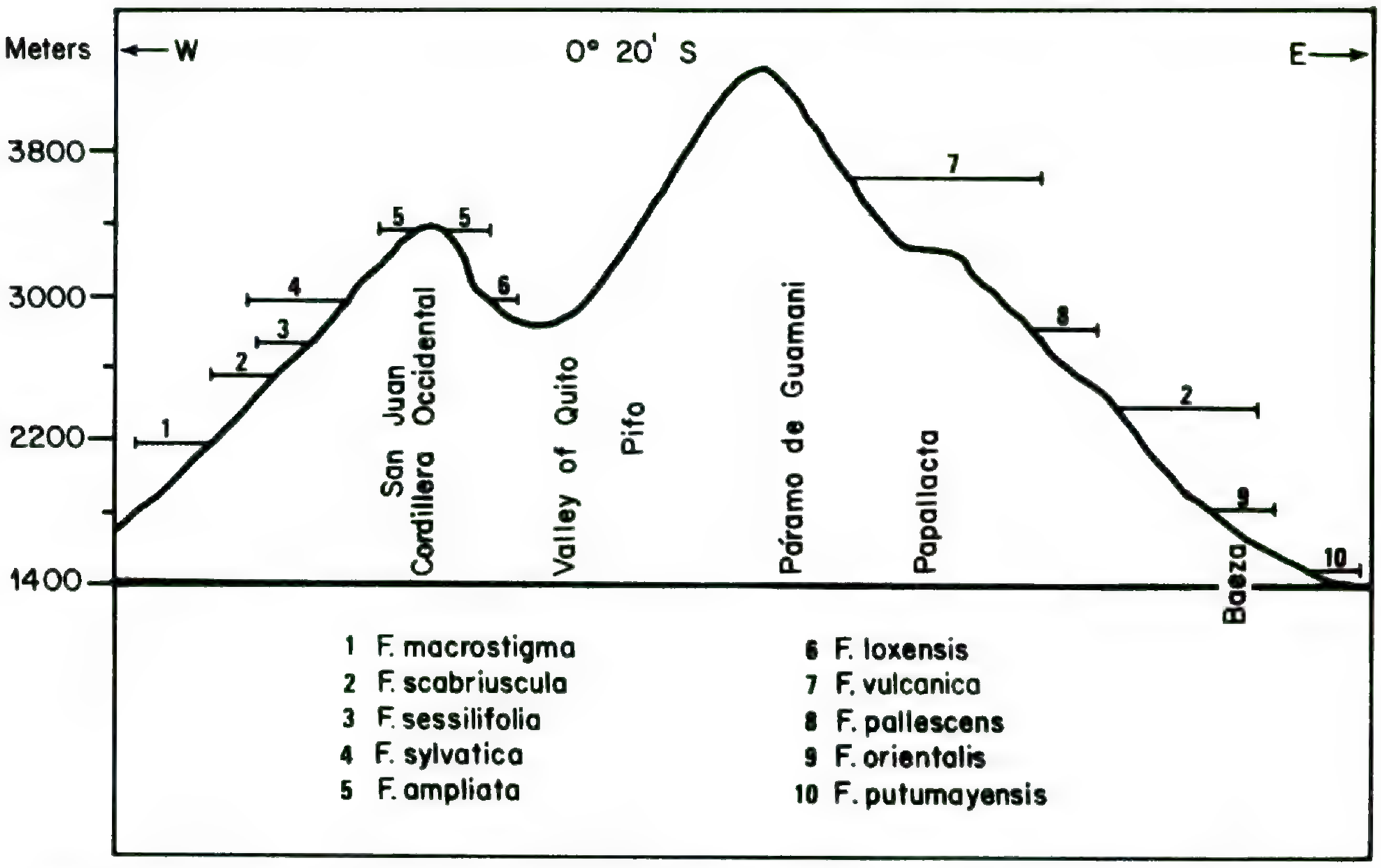


FIGURE 9. Altitudinal zonation of *Fuchsia* along a transect crossing the Ecuadorian Andes in Prov. Pichincha and Napo.

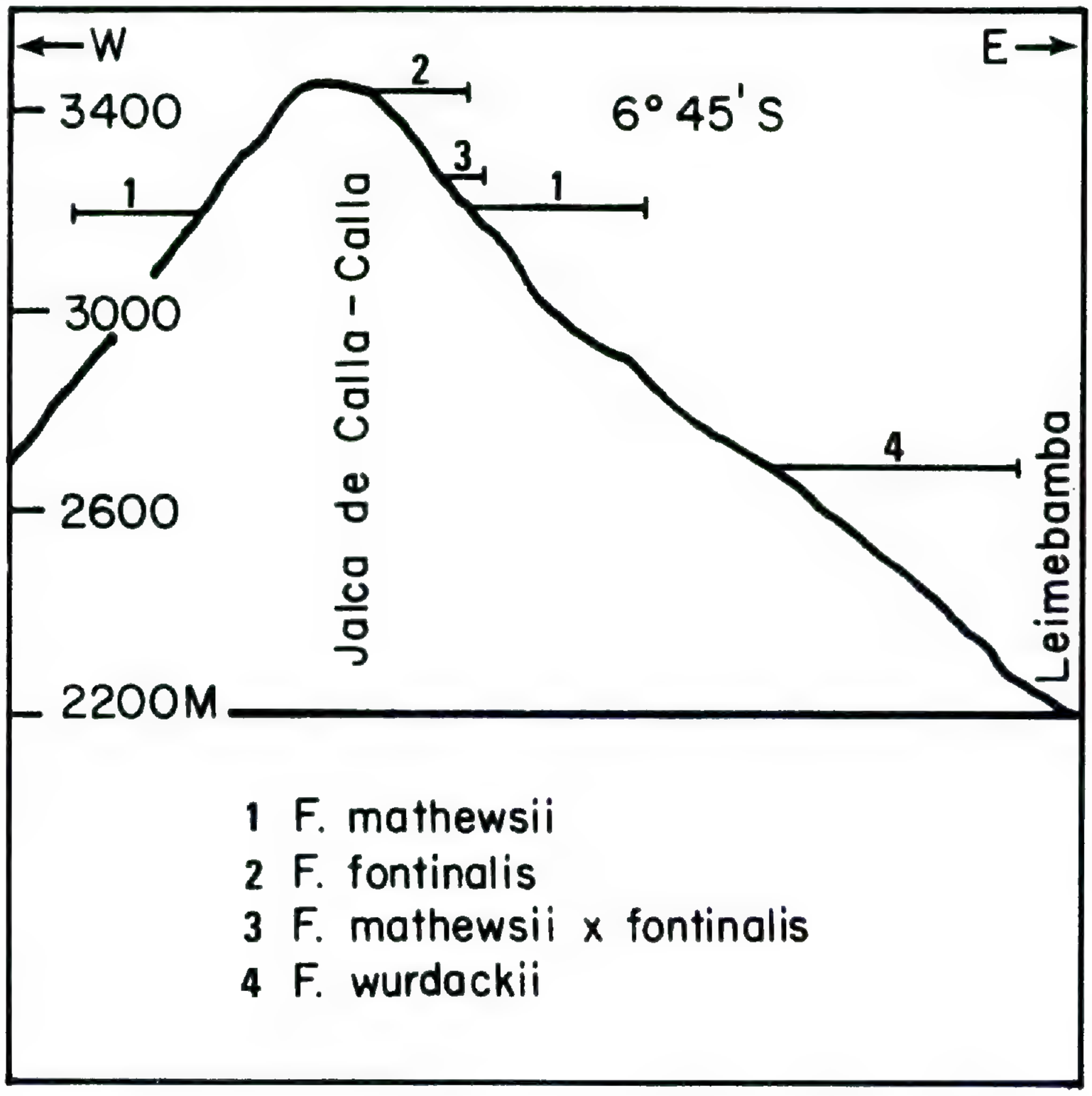


FIGURE 10. Altitudinal zonation of *Fuchsia* along a transect crossing the Cerro de Calla-Calla, Dept. Amazonas, Peru.

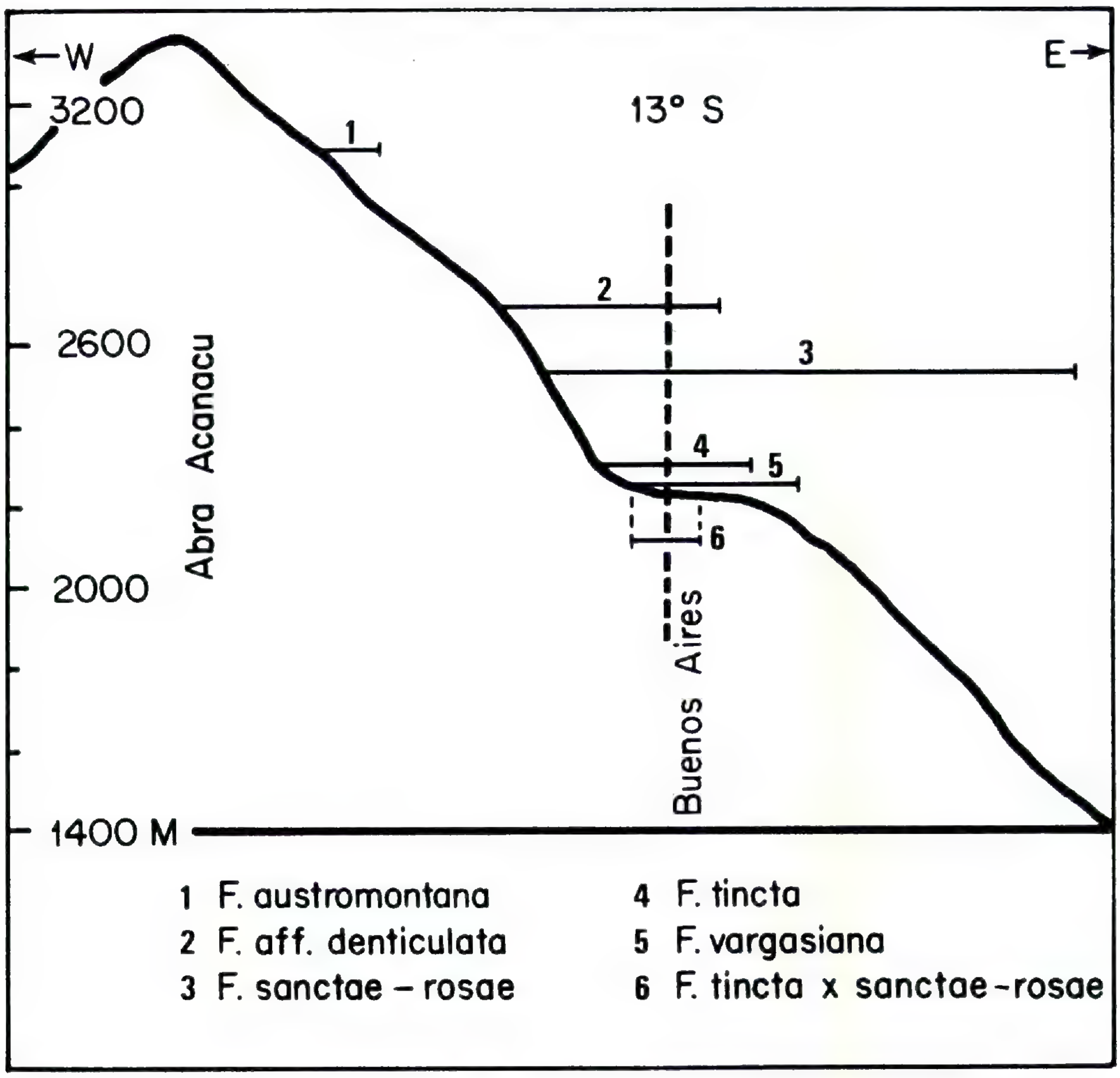


FIGURE 11. Altitudinal zonation of *Fuchsia* along a transect on the eastern slopes of the Peruvian Andes in Dept. Cuzco, Prov. Paucartambo. The vertical dashed line indicates the high degree of sympatry in the vicinity of Buenos Aires.

have been detected on high peaks of the tropical Andes, and detailed palynological evidence from the northern Andes (Hammen, 1974) shows that a maximum temperature depression of 7°C and a lowering of the upper elevation vegetation zones by 1,200–1,500 m occurred during recent glacials (Fig. 13). Glacial episodes were often accompanied by much drier periods than at present. The implications of these climatic fluctuations are complex and different for plants of different altitudes and humidity regimes. For instance, páramo organisms, as well as those adapted to dry, lowland habitats, experienced periods of range extension and secondary contact during the glacials. Moist lowland taxa, on the other hand, underwent isolation and differentiation during glacial episodes. During interglacials such as at present, the dry lowland and high páramo organisms became restricted to island-like enclaves.

The preceding events regarding the recent history of the Andes have several important biogeographical and evolutionary implications for sect. *Fuchsia*. First, assuming that the ancestors of sect. *Fuchsia* were adapted to cool temperate

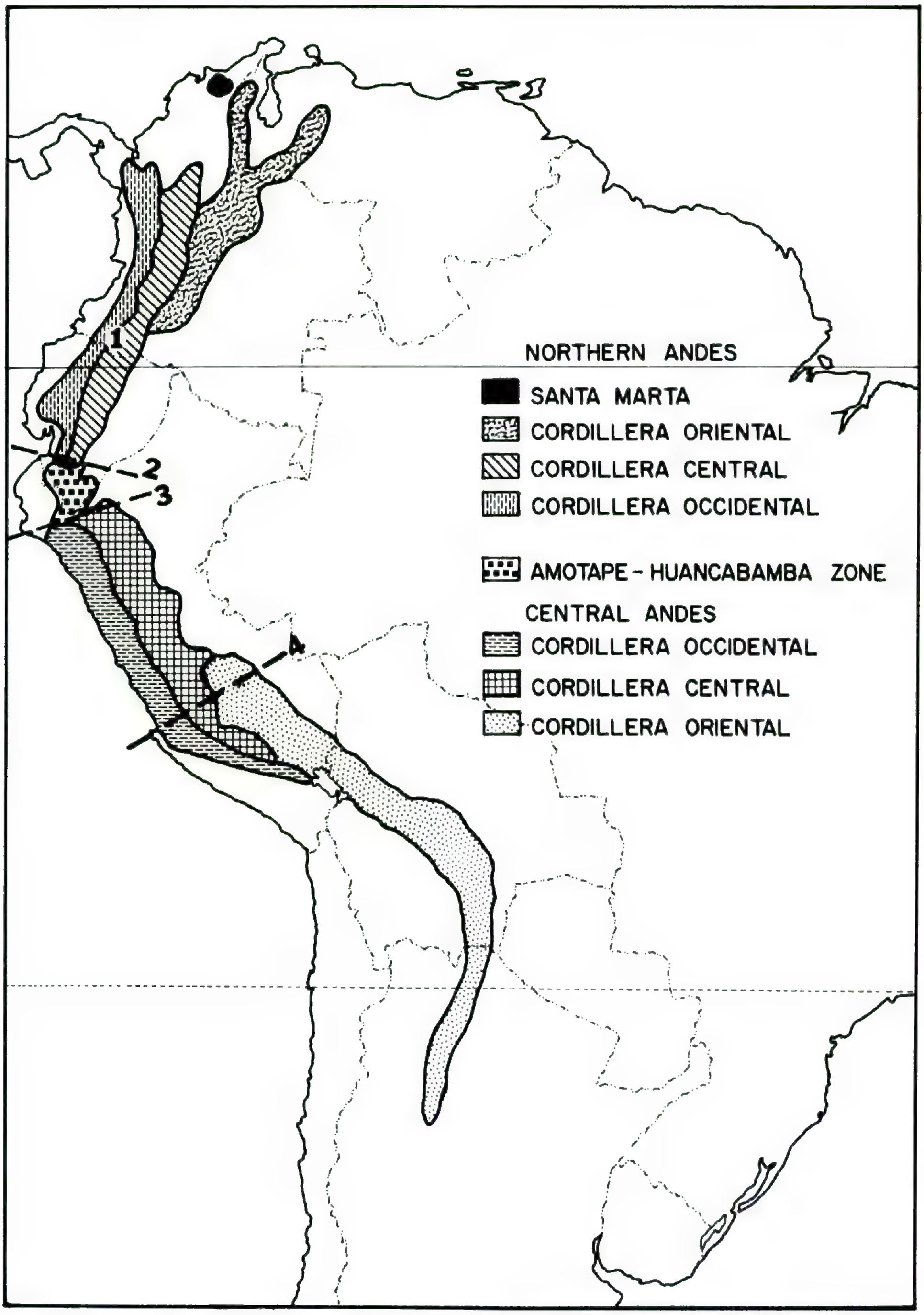


FIGURE 12. Major structural units of the Andes where *Fuchsia* sect. *Fuchsia* occurs. Adapted from Simpson (1979) and Sillitoe (1974). 1 = Nudo de Pasto. 2 = Amotape zone, the northern limit of the Central Andes and a major tectonic segment boundary, aligned to the west with the Carnegie Ridge and the Gulf of Guayaquil. To the north a marked change in the geology of the Andes occurs, with a line of recent stratovolcanos. 3 = Huancabamba deflection. 4 = Pisco or Abancay deflection, marked by a major step in the coastline, a shallowing of the Peru-Chile trench, and the offshore Nazca Ridge.

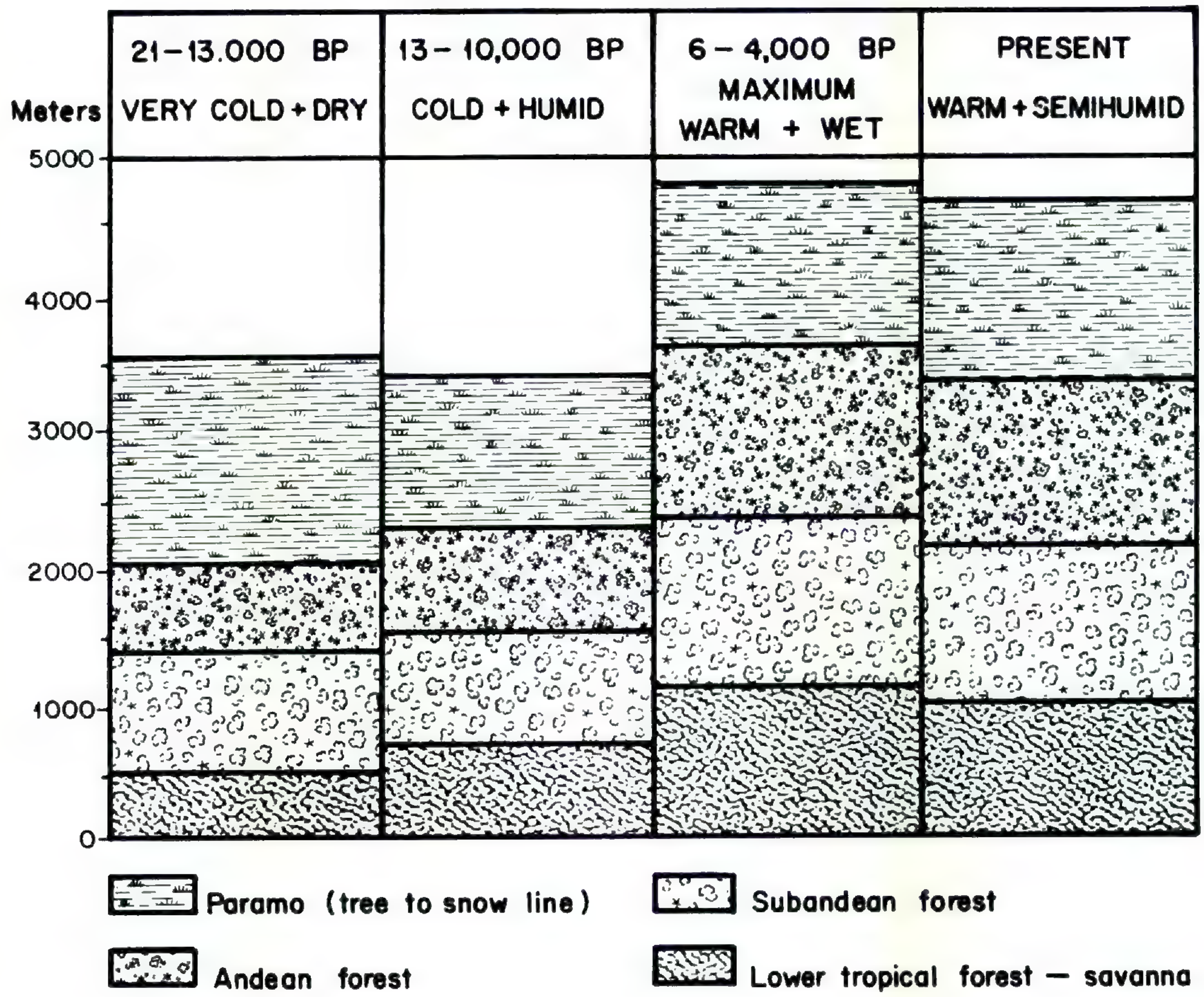


FIGURE 13. Effects of recent climatic fluctuations upon the vegetation zones in the Cordillera Oriental of Colombia. Adapted from Hammen (1974) and Lauer (1979).

habitats as are almost all the extant species in the genus, they could not have arrived in the tropical Andes until the Miocene, and major opportunities for the colonization of Andean forest habitats probably did not arise until the early Pliocene. Second, the glacial periods of the Pleistocene were probably times of range extension and secondary contact for populations of *Fuchsia* that would be comparatively isolated at interglacials such as at present. Though the drier climatic conditions of most glacials would negatively affect mesic groups such as *Fuchsia*, the considerable lowering of the montane vegetation zones (up to 1,500 m lower for Andean forest in the coldest glacials) would cause a great increase in its horizontal distribution, making possible migration and secondary contact of taxa across areas presently occupied by lowland vegetation. Third, a comparison of the species compositions of the different Andean structural units where *Fuchsia* sect. *Fuchsia* occurs should enable us to analyze the nature and directions of some of the migrations that have taken place in the section.

Patterns of distribution. *Fuchsia* is a common element of the cloud forest belt that extends along the eastern slopes of the Andes from northern Colombia and Venezuela to northern Argentina and along the west side of the Andes from Venezuela to northern Peru. The geology and physiognomy of the different struc-

tural units of the Andes have been summarized by Simpson (1975b) and Duellman (1979). The structural units where *Fuchsia* sect. *Fuchsia* occurs are shown in Figure 12. Two basic changes from Simpson's (1975b and 1979) system are introduced, however. First, a small unit called the Amotape-Huancabamba zone is added because both the Amotape zone in southern Ecuador (as treated in Sillitoe, 1974) and the Huancabamba deflection in northern Peru constitute clearly defined tectonic boundaries where major changes in the overall geology of the Andes occur (Sillitoe, 1974). It is therefore misleading to extend the structural units of the Northern Andes south of the Amotape zone to the Huancabamba deflection or to extend those of the Central Andes north of the Huancabamba deflection into Ecuador. Though several authors considered the Huancabamba deflection to be the main north-south migration barrier in Andean organisms (Vuilleumier, 1971; Simpson 1975b, 1979; Duellman, 1979), this is least true for cloud forest organisms. The 21 species of amphibians and reptiles that occur both north and south of the Huancabamba deflection are primarily cloud or wet forest inhabitants on the eastern slopes of the Andes (Duellman, 1979). In sect. *Fuchsia* and perhaps in other cloud forest organisms, it is perhaps more appropriate to treat the entire Amotape-Huancabamba zone as the transitional area between the species of the Northern and Central Andes.

The second change is the separation of Simpson's (1975b, 1979) "Cordillera Oriental" of the Central Andes into two units, the Cordillera Central to the north and the Cordillera Oriental to the southeast. This aids our analysis of species distributions by producing three units in the Central Andes that are comparable in size and extent to the units of the Northern Andes. Tectonically and geologically, however, there are ample reasons for this division as well. The dividing line of the two units corresponds to the Pisco or Abancay deflection (Fig. 12), which is marked on the western side by the offshore Nazca ridge, a major step in the coastline, and a shallowing of the offshore Peru-Chile trench. Along the boundary in the mountains to the east, there is a marked northward narrowing of the cordilleras, a change in direction of the Eastern Cordillera, and important changes in the Mesozoic paleogeography (Sillitoe, 1974).

Figure 14 summarizes the species and species group distributions in the different structural units of the Andes where sect. *Fuchsia* occurs. The following discussion deals with the species relationships of each unit. Reference is also made to species distribution maps (Figs. 55–67) in order to explain patterns observed within and between the structural units.

Northern Andes

Sierra Nevada de Santa Marta. This is a small, isolated volcanic range and the northernmost segment of the Andes. It has undergone a complex geological history, but the Sierra Nevada de Santa Marta was underwater until the Miocene and apparently experienced its major upheaval in the Quaternary (Simpson, 1975b). The sole species of sect. *Fuchsia* that occurs there is *F. magdalenae,* which is endemic to the Andean forest and subpáramo of this small, but high, mountain massif. General floral characters place this species closest to the Peruvian-centered *F. denticulata* species group, but it is very unusual in the section because

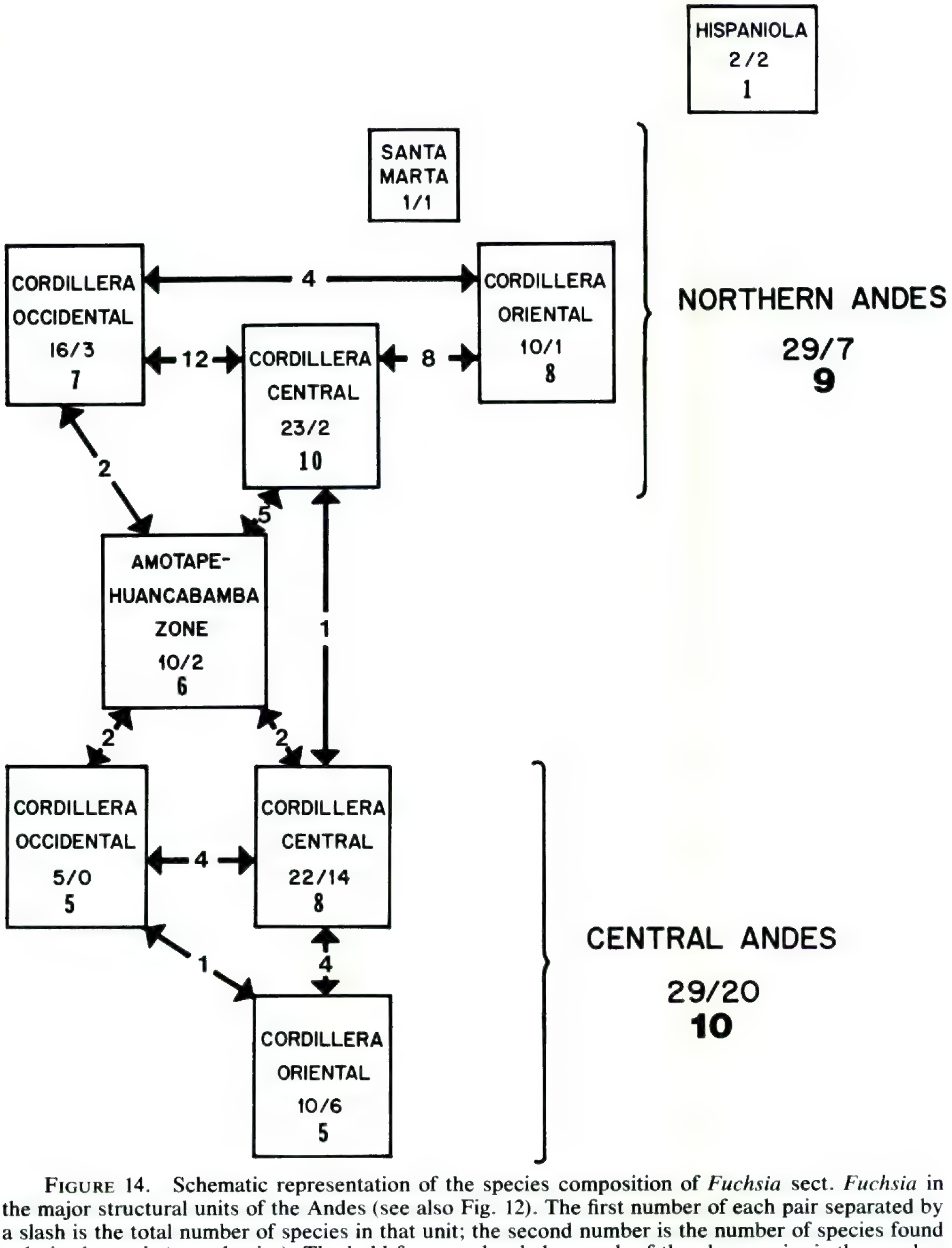


FIGURE 14. Schematic representation of the species composition of *Fuchsia* sect. *Fuchsia* in the major structural units of the Andes (see also Fig. 12). The first number of each pair separated by a slash is the total number of species in that unit; the second number is the number of species found only in that unit (= endemics). The bold face number below each of the above pairs is the number of species groups present in that unit. Numbers of species shared by two units appear between the arrows connecting different units.

of its tetraploidy with biporate pollen and its smooth, non-annular nectaries. Although suitable habitats for *Fuchsia* are found less than 40 km away across the Cesar depression in the Sierra de Perijá of the Cordillera Oriental, the only species of the genus that occurs there is *F. gehrigeri,* which bears no close

relationship to *F. magdalenae* and is found elsewhere only in the Mérida Andes of Venezuela. Mayr (1963) has noted that peripheral isolates of many genera show one or more of the following characters: they usually occur in a small geographical area, have low absolute population sizes, and differ from the main body of the species in several, often unique morphological or other characters, criteria that apply well to *F. magdalenae*.

Cordillera Oriental. This unit is characterized by a comparatively low number of species but a high number of species groups, low endemicity, and strong east-west and north-south connections to neighboring cordilleras.

As shown by van der Hammen's detailed geological and palynological studies of the Cordillera Oriental of Colombia (Hammen, 1974) this unit was uplifted to nearly its present level in the mid- to late Pliocene, followed by a long sequence of glacials and interglacials during the Pleistocene. Through the examination of lacustrine sediments, van der Hammen and coworkers were able to document recent climatic extremes. During the Last Glacial, at 21,000 years BP, the climate around the high plains of Bogotá became extremely cold and dry, with a ca. 7°C temperature depression and a 1,200–1,500 m vegetation zone lowering compared to the present. In the Middle Holocene, a "hypsothermal" occurred in the current interglacial when the temperature became 2°C warmer and the vegetation zones several hundred m higher than at present. The average effects of these climatic changes on the altitudinal distribution of different vegetation zones are illustrated in Figure 13.

Considering the magnitude of the vegetation zone fluctuations during the Pleistocene, migrations of *Fuchsia* across the Magdalena and Cauca River valleys to the Cordilleras Central and Occidental could have occurred almost without interruption or via bird dispersal across short lowland barriers. At present, there is only a 35 km gap between the 1,000 m contours of the Cordillera Central and the Cordillera Oriental at 5°N Latitude, which is the approximate latitude of Bogotá and where *F. hirtella*, *F. petiolaris*, and *F. venusta* are found in both cordilleras. These species are all more common in the Cordillera Oriental than in the Cordillera Central, and they most likely migrated in a westerly direction to attain their present distribution there. The distribution patterns of the large páramo genera *Espeletia* and *Puya* give strong evidence of the same pattern of a Cordillera Oriental source area with subsequent migrations to the Cordillera Central (Cuatrecasas, 1979). The recent origin of these páramo genera (Hammen, 1979) further supports the idea that the Pleistocene was an important period for plant migrations in the Andes.

In its southern extreme, the Cordillera Oriental abuts the Cordillera Central just north of the Nudo de Pasto. Also known as the Macizo Colombiano, the Nudo de Pasto (Fig. 12) is a high massif in southern Colombia and northernmost Ecuador that has acted as a very effective migration corridor for Andean species that spread into the three different units that diverge northwards from it. Several species of *Fuchsia* have present day distributions that indicate they used this corridor to reach the southern part of the Cordillera Oriental from the south. These include *Fuchsia sessilifolia* (Fig. 63), *F. scabriuscula* (Fig. 56), and *F. cuatrecasasii* (Fig. 58). The first of these species probably used the Nudo de

Pasto as a corridor to spread northwards into all three units of the Northern Andes. *Fuchsia verrucosa* (Fig. 65), which is centered in the Cordillera Oriental, has a distribution indicating that it migrated southwards along the eastern edge of the Nudo de Pasto to reach its present locations in the Cordillera Central in southern Colombia.

In the north, the Cordillera Oriental splits into two ranges near the Colombian-Venezuelan border, the Sierra de Perijá to the north, and the Mérida Andes to the northeast. The Mérida Andes are separated from the Colombian Andes by the low Táchira depression, which constitutes a secondary dispersal barrier within this unit. Six species occur just on the Colombian side of the barrier, and the only endemic species in this unit, *F. gehrigeri,* is found only in the Mérida Andes and the Sierra de Perijá.

In summary, the distribution patterns of this unit show close ties to the adjacent Cordillera Central, with all but one species and numerous species groups shared between them. The presence of so many species in common and their relative lack of differentiation in the different cordilleras suggests that they have not been separated for very long or that they have been in secondary contact, and it is shown how Pleistocene climatic changes could easily account for migrations or secondary contact of species between the two cordilleras.

Cordillera Central. This unit has the highest representation of species and species groups, yet the next lowest proportion of endemism of any structural unit. This is largely due to the central position of this unit in the Northern Andes and its close proximity to three adjacent units. The more gently sloping eastern flanks of the Cordillera Central offers a greater variety of habitats than the comparatively steep slopes of the Cordillera Occidental.

Twelve species are common to both the Cordillera Central and the Cordillera Occidental. The high interandean valleys of Ecuador, the Nudo de Pasco, and the high plateau separating the Cauca and Patía Rivers are major corridors for species exchange between these two units, and they all must have greatly facilitated migration of upper montane species during Pleistocene glacials.

The *Fuchsia petiolaris* species group, which is strongly centered in the Cordillera Central, has complex patterns of variability between populations and is the source of considerable taxonomic confusion. In Ecuador, populations of this species group are found on many of the high, semi-isolated peaks that are found in both cordilleras (Fig. 59). Since members of this group typically occur at high elevations near tree line, they were probably more strongly affected by Pleistocene events than other groups in the section; Sauer (1971) recorded three main glaciations in Ecuador. The *F. dependens* species group also developed strongly in a relatively small area centered in the Cordillera Central in southern Colombia (Fig. 66).

Cordillera Occidental. Seventy-five percent of the species in this unit are shared with the Cordillera Central, while only three species are endemic there. *Fuchsia sylvatica* occurs on the Pacific slopes in Ecuador and is vicarious with *F. nigricans,* which is found in the same cordillera but north of the Patía River valley in southern Colombia. *Fuchsia macrostigma,* however, occurs on both sides of the Patía River, which is a secondary migration barrier within this unit. Two of the

endemic species, *F. cinerea* and *F. polyantha,* are very localized and occur on the edge of the Nudo de Pasto.

Amotape-Huancabamba Zone

Despite its relatively small area (Fig. 12), this unit has the same number of species as the much larger Cordillera Oriental of the Northern Andes. This reflects its key position bordering four different structural units, as well as the equatorially based center of species diversity in the section. *Fuchsia glaberrima* is the only species that occurs both north and south of this unit. The Amotape-Huancabamba Zone thus constitutes the major transitional zone between the species of the Northern and Central Andes. The species found within this unit, however, are a mixture from all four adjacent structural units and include two endemic species. This area is still insufficiently collected because of its inaccessibility, and future explorations will be certain of finding novelties in *Fuchsia*. One of the most distinctive species in the section, *F. steyermarkii,* occurs there and appears to be most closely allied to species from the Cordillera Central in northern Peru.

Central Andes

Cordillera Occidental. The cloud forest belt on the western side of the Andes ends near the Peruvian-Ecuadorian border. As a result, most of the Cordillera Occidental in Peru is too dry for *Fuchsia,* and four of the five species present in this unit are only found north of 8°S Latitude. These species inhabit local patches of mesic forest that is more a mixed scrub than true cloud forest. *Fuchsia ayavacensis* is the only species that is largely restricted to this unit, and it forms part of the northern *F. petiolaris* species group. Three of the species in the unit are shared with the Cordillera Central of Peru and probably were dispersed across the Marañón River valley from the east. At present, there are only approximately 25 km separating the closest populations of *F. mathewsii* on either side of the Río Marañón. The genus *Ascidiogyne* (Compositae) provides another interesting example of this trans-Marañón disjunction (Cuatrecasas, 1979). This unique genus has only two species, one in the high "jalca" of Dept. Amazonas in northern Peru, and the other across the Marañón valley to the west in Dept. Cajamarca.

Fuchsia denticulata is an exceptional species in this unit because it is found between 9°S and 13°S Latitude in isolated pockets of mesic vegetation on the otherwise arid Pacific slopes of Depts. Lima and Ancash. This species is widespread on the eastern slopes of the Andes, however, from Dept. Huánuco in Peru to Dept. Cochabamba in Bolivia. This disjunct pattern was previously discussed by Simpson (1975b, 1979) for other mesic Andean species. Simpson (1975a) postulated that the high parts of the Cordillera Occidental and its upper western slopes experienced heavier precipitation during Pleistocene glacial periods than at present. At these times, east-west migrations of mesic montane plant taxa were made possible across the "nudos" or low connecting paths between the Pacific and Amazonian slopes of the Peruvian Andes. *Fuchsia denticulata* is a clear example of migration directly across the Andes via the Nudo de Pasco, at the

latitude of Lima. There are fewer than 100 km (air distance) now separating the closest populations of *F. denticulata* on the western slopes above Lima and on the eastern slopes in Dept. Junín (Fig. 61). Besides its presence in cloud forests of the Cordillera Central in Junín, *F. denticulata* also occurs in higher interandean valleys such as the valley of Comas, which has an intermediate habitat type between the eastern "ceja" and the small mesic pockets restricted to protected canyons on the western slopes. This distribution pattern suggests how species with wide ecological tolerances may have been able to cross the Nudo de Pasco under more humid conditions than exist at present. Once *F. denticulata* reached the Pacific slopes, it probably spread north (and south?) in what may have been a continuous moist forest belt during Pleistocene glacials (Simpson, 1975a, 1979). Other species such as *Arracacia incisa* Wolff. (Umbelliferae) show the same pattern as *F. denticulata,* and Simpson (1975b) gave several examples of species that are presently disjunct between the western slopes above Lima and the eastern slopes further south near Cuzco. These latter species may have used a more southern pass, the Nudo de Vilcanota.

Cordillera Central. This unit has almost as high a species diversity as the Cordillera Central of the Northern Andes, but two fewer species groups and a much higher proportion of endemic species. It is much more dissected and is in contact with fewer units than the northern Cordillera Central. The adjacent Cordillera Occidental is too dry to allow major opportunities for the establishment of new populations of *Fuchsia,* and strong migratory barriers are present to the north in the Huancabamba depression and to the south in the Río Apurimac valley. Though there are proportionately fewer species groups present in this unit than in most others, at least half of those groups present are restricted or strongly centered here. All four species of the *F. simplicicaulis* species groups are endemic to the Cordillera Central, as are all but one species each of the *F. macrophylla, F. boliviana,* and *F. decussata* species groups. Speciation has probably been facilitated by the presence of several semi-isolated ranges such as the Cordillera Azul on the Huánuco-Loreto border. Five very localized endemics are concentrated in Dept. Amazonas of northern Peru.

Cordillera Oriental. As in the Cordillera Oriental of the northern Andes, ten species of *Fuchsia* occur in this unit, but a lower number of species groups and a much higher proportion of endemic species are found here. The Cordillera Oriental of Peru and Bolivia is more isolated from other units where sect. *Fuchsia* occurs than the northern cordilleras. Four species, *F. boliviana, F. austromontana, F. denticulata,* and *F. sanctae-rosae,* occur from southern Peru into Bolivia, showing the continuity of distribution of most species in this unit across the outer slopes of the Titicaca Basin. *Fuchsia boliviana* just barely extends north of the Río Apurimac into the Cordillera Central, and it may only be naturalized there. *Fuchsia tincta* and *F. vargasiana* are restricted to one or two valleys in southern Peru, but are very closely related to the Bolivian *F. furfuracea. Fuchsia macrophylla* and *F. decussata* are both centered in the Cordillera Central and just enter the northern part of the Cordillera Oriental. The only species group of this unit that reaches the northern Andes is the *F. denticulata* group.

Hispaniola

Two species of sect. *Fuchsia* are widely disjunct from the rest of the species in the section and are endemic to the Caribbean island of Hispaniola. A similar Andean-Hispaniola disjunction of montane species has recently been reported by Cuatrecasas (1979) for the genus *Laestadia* (Compositae), which has four species in the Andean páramos, one in high elevation Costa Rica, and one on Hispaniola. The ancestors of the fuchsias on Hispaniola probably reached the island from South America by long distance bird dispersal, a mechanism that has been proposed to account for other disjunctions in the genus, such as *F. cyrtandroides* on Tahiti. Judging from the lack of clear affinities of either of the two Hispaniola species to any species group on the South American mainland, their arrival to the island does not appear to be recent. It is furthermore unclear whether *F. triphylla* and *F. pringsheimii* were derived from a common ancestor or whether they arrived separately, by a "double invasion" in the sense of Mayr (1963). Supporting the possibility of a common ancestor, both species have the combination of tetraploidy with biporate pollen, which is unusual in the genus. In addition, they are presently isolated altitudinally throughout their range, except in certain contact areas where partly fertile hybrids are formed. On the other hand, the two species differ widely in morphological characters (Table 19). *Fuchsia triphylla* is morphologically similar to the main body of Andean species of sect. *Fuchsia*, but *F. pringsheimii* has several floral characters not clearly related to any section in the genus, such as particular non-annular nectaries and very large, emarginate petals. If a double invasion did occur, then *F. pringsheimii* is most likely the descendant of the earlier immigrant, and its unique assemblage of characters may even be derived from the early offshoot of the genus that had reached Central America.

Summary of Distribution Patterns

A small number of taxa in *Fuchsia* sect. *Fuchsia* show wide disjunctions in range from the main body of species in the Andes or from other members of their species groups. These include species such as *F. magdalenae* in the Sierra Nevada de Santa Marta and *F. triphylla* and *F. pringsheimii* on Hispaniola. These species show fundamental differences from each other and from the main body of the section in several morphological and cytological features. In this way, they can be considered peripheral isolates in the sense of Mayr (1963) and may represent early offshoots of the section that were isolated at the margins of the range.

In the contiguous structural units of the Andes where the bulk of the species in sect. *Fuchsia* are concentrated, a major change in the species and species group composition occurs in southern Ecuador and northern Peru in a transitional area called the Amotape-Huancabamba zone. Only one species and four species groups occur both north and south of this area. Consequently, it has been possible to compare the distribution patterns of the species in the Northern Andes with those of the Central Andes.

As seen in Figure 14, the Northern and Central Andes each have 29 species and nearly the same number of species groups. The structural units with the greatest number of species are the Cordillera Central of the Northern Andes and

the Cordillera Central of the Central Andes. While we cannot place the center of diversity of the section in either one of these two areas, it is clearly located on the eastern slopes of the Andes in Ecuador and northern Peru. From there, we find a gradual reduction in species number to the north and south in a pattern analogous to the distribution of hummingbird species (Skutch, 1973).

Just over half (32 of 61) of the species in sect. *Fuchsia* are restricted to a single structural unit of the Andes or to the island of Hispaniola. As might be expected of easily dispersed plants in the cloud forest belt, this proportion is lower than that normally observed in páramo plants, where high degrees of local endemism are common (Simpson, 1975b; Cuatrecasas, 1979). The proportion of endemics (= species limited to a single structural unit) in sect. *Fuchsia* varies significantly, however, between the Northern and Central Andes. In the Northern Andes, with 24% endemics, migration between structural units has been facilitated by the proximity of the three cordilleras and the numerous corridors that would be available in glacial periods of lowered vegetation zones. Accordingly, four species in the Northern Andes are present in all three cordilleras, and twelve are found in two cordilleras. In contrast, the Central Andes have 69% of the species endemic, with only one species present in all three cordilleras and five in two cordilleras. The Central Andes have much stronger migration barriers because of the greater spatial isolation of the Cordilleras Central and Oriental, and the aridity of the Cordillera Occidental.

The key migratory corridor in the Northern Andes has been the Nudo de Pasto (Macizo Colombiano). The three northern cordilleras merge at this massif, and many species have used it to disperse latitudinally or longitudinally into the different structural units. A total of 14 species are present along the Nudo de Pasto (as defined by Duellman, 1979), which is the richest local species concentration of sect. *Fuchsia* in the Andes.

Although the Cordillera Oriental of the Northern Andes is poorer in species number than the adjacent Cordillera Central, it has been an important source area of several species present in the northern part of the Cordilleras Central and Occidental. At least three species have migrated westwards across the Magdalena valley, and one or two migrated further west across the Cauca valley into the Cordillera Occidental. In Ecuador, the opportunities for migration between the two cordilleras have been numerous, and it is difficult to determine for most species in which direction they may have spread.

Most species groups of the Central Andes are restricted to a single structural unit, but three migration paths between different structural units were identified, 1) the western migration of two or three species across the Marañón River in northern Peru, 2) the western migration of *Fuchsia denticulata* across the Andes to the Pacific slopes via the Nudo de Pasco, and 3) the southern expansion of two species from the Cordillera Central into the Cordillera Oriental.

Secondary barriers exist within many structural units that have also been important filters to migration. For example, only three of ten species in the Cordillera Oriental of the Northern Andes occur on both sides of the Táchira depression in western Venezuela. Similarly, the Patía River valley in southwestern Colombia and the Huallaga and Mantaro Rivers in central Peru have also acted as selective barriers within their respective units.

REPRODUCTIVE BIOLOGY

FLORAL BIOLOGY

The maturation sequence of flowers seems to be similar in all species of sect. *Fuchsia*. Anthesis usually occurs in the early morning, at which time the stigmatic surface becomes wet with a sticky exudate and is presumably receptive (Raven, 1979a). Anther dehiscence is usually delayed from several hours to one or two days, depending on the species, but the stigma remains receptive in all species until after the anthers open; protogyny is ubiquitous but does not preclude self-pollination. Flowers last an average of three to four days from anthesis to abscission. A spatial separation of 2–20 mm usually exists between the stamens and the exserted stigma, further reinforcing outcrossing. Notable exceptions, however, are *F. boliviana*, *F. nigricans*, and *F. verrucosa*, in which at least some populations have the stigma in close contact with the upper staminal whorl. In other species, if no pollinator visits are made before anther dehiscence, the stigma-anther separation is usually small enough that wind or other mechanical factors are sufficient to cause self-pollination. Self-pollination is favored because the pollen is held together in elastic strings by their viscin threads and because the stigma is situated below the anthers in the hanging flowers that characterize sect. *Fuchsia*.

As far as known, all species of *Fuchsia* are self-compatible, which is considered an advanced character state in the family (Raven, 1979a). *Fuchsia* is the only genus in the family in which marked protogyny occurs. Although Raven (1979a, p. 578) reports protogyny in *Circaea*, it is barely pronounced and therefore not really comparable to the protogyny found in certain sections of *Fuchsia*.

Controlled crosses in both native and naturalized populations of *F. boliviana* show that this species is self-compatible and largely autogamous. The high degree of autogamy is probably exceptional in the section and undoubtedly helps to account for the widely naturalized distribution of *F. boliviana* at present. In this species, protogyny is very poorly developed, and the anthers and stigma are in close contact; naturalized populations at El Junquito, Venezuela, were found to self-pollinate in bud.

Male sterility is an outcrossing device that is found in the Onagraceae only in certain sections of the genus *Fuchsia*. All the known sections with male sterility are small and have distributions that are peripheral to the main Andean-Brazilian center of the genus. One possible case of gynodioecy has now been found in sect. *Fuchsia*, however. Certain populations of *F. hartwegii* from several different localities in Colombia include male-sterile individuals. Other populations of the same species apparently consist entirely of hermaphroditic plants. A similar situation has recently been documented in *F. paniculata* (sect. *Schufia*) of Central America (Breedlove et al., 1982). Further field work and breeding studies are needed to clarify the situation of male sterility in *F. hartwegii*, but its confirmation would constitute the fifth independent occurrence of male sterility in the genus.

POLLINATION

Table 3 shows the features of sect. *Fuchsia* that strongly associate it with hummingbird pollination. In addition, the beaded viscin threads, which enable

TABLE 3. Characters of *Fuchsia* sect. *Fuchsia* adapted to hummingbird pollination.

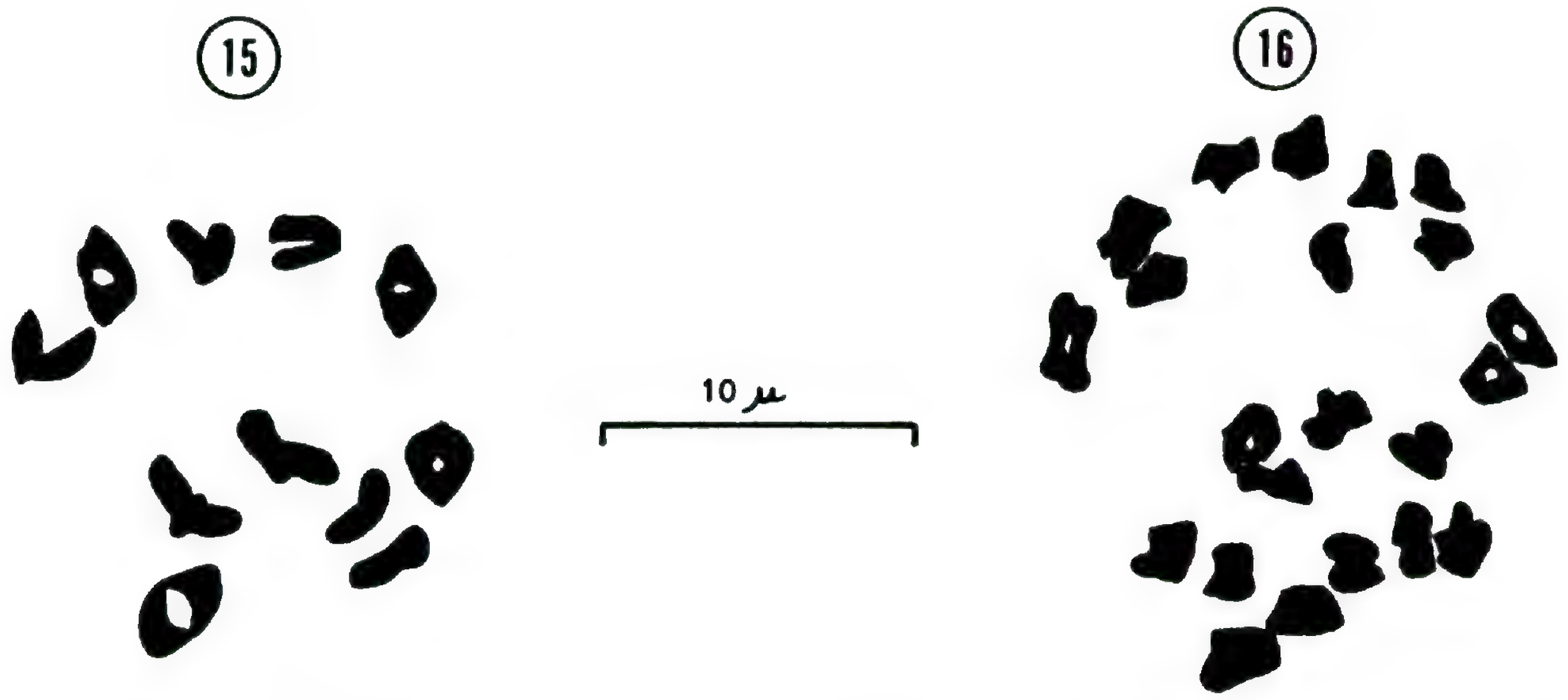
	Hummingbirds[1]	*Fuchsia* sect. *Fuchsia*
Distribution:	New World, highest diversity in the tropical Andes.	Tropical Andes, Hispaniola
General behavior/ phenology:	Tropical species are non-migratory, territorial, diurnal.	Plants long-lived with diurnal anthesis, long-lived flowers (av. 3–4 days), and long flowering season.
Pollination-related characters:	Poor sense of smell, preference for red coloration, long bill and sucking tongue, hovering approach, high energy requirement, and frequent daily feeding.	Flowers odorless, reddish, tubular, divergent to pendulous, copious nectar production.

[1] From Grant & Grant, 1968; Percival, 1969; Raven, 1972a.

hundreds of grains to be removed in a single bundle, appear to be of adaptive value in bird pollination (Percival, 1969; Skvarla et al., 1978). The hummingbirds feed on the nectar that is produced at the base of the floral tubes, and, unlike many groups of insects, they remain active in the rain and at cool temperatures, an obvious advantage for montane cloud forest groups such as *Fuchsia* (Heinrich & Raven, 1972).

Only incidental observations were made on pollination in *Fuchsia* during the course of field work. Numerous unidentified hummingbird species were seen visiting different species of *Fuchsia* sects. *Fuchsia* and *Hemsleyella*, and no non-avian visitors were observed. On Hispaniola, there are two species of *Fuchsia* that occur at different altitudes and three resident species of hummingbirds. *Chlorostilbon swainsonii*, which is the "large highland species" of Lack's (1976) niche theory of West Indian hummingbirds, feeds exclusively below the canopy (Lack, 1976) and has been photographed visiting *F. triphylla* (Fig. 32). Lack's "large lowland species," *Anthracothorax dominicus*, is actually present in the highlands there, but is restricted to the tree canopies. The third "small species" completing the hummingbird fauna of the island is *Mellisuga minima*, which occurs at all elevations. But because it is the second smallest bird in the world it is therefore very unlikely to pollinate the moderately long-tubed *F. triphylla* and *F. pringsheimii*. The hybrids found between these two species of *Fuchsia* in areas where their altitudinal limits are in close proximity can almost certainly be attributed to visits by *Chlorostilbon*, which ranges throughout the elevational ranges of both species and occupies the understory niche almost exclusively.

Naturalized populations of *F. boliviana* were observed over a several day period in March 1979, at El Junquito and Colonia Tovar, Venezuela. Two different populations were aggressively defended and visited throughout the day by the long tailed sylph, *Aglaiocercus kingi*. None of the visits were legitimate pollinations, however, because the hummingbird consistently pierced the base of the tube and robbed the flowers of their nectar. At higher elevations in the Colonia Tovar, the same species of *Fuchsia* was visited by the booted racket-tail, *Ocreatus underwoodii*, which appeared to be making legitimate visits without piercing the tube.



FIGURES 15–16. Meiotic chromosomes in *Fuchsia* sect. *Fuchsia*, metaphase I.—15. *F. loxensis*, $n = 11$, from *Berry 3133* (MO).—16. *F. verrucosa*, a tetraploid, $n = 22$, from *Berry 3662* (MO).

In several cases two closely related species differ mainly in floral tube length and coloration, yet occur together or in close proximity without the presence of intermediate plants. *Fuchsia polyantha*, which has red flowers 34–43 mm long, grows with *F. sessilifolia*, which has pale pink tubes 13–20 mm long. A similar pattern is found between *F. tincta* and *F. vargasiana*, and between *F. macrophylla* and *F. macropetala*. This pattern suggests that hummingbird species are species-specific pollinators of *Fuchsia*, the specificity linked to tube lengths and color patterns, or that flower dimensions mechanically act against interspecific pollination. In hawkmoth-pollinated species of *Oenothera*, Gregory (1964) found that short-tubed flowers were only effectively pollinated by short-tongued hawkmoths, but long-tubed species were able to use long-tongued as well as short-tongued hawkmoths as effective pollinators.

Further observations on the pollination system of sect. *Fuchsia* are needed and could analyze specific problems such as the degree of specificity between hummingbirds and *Fuchsia* species, the relation of bill length to tube length, the importance of territoriality of hummingbirds in pollen dispersal, and the possible presence of insect pollinators.

VEGETATIVE REPRODUCTION

Trailing stems or broken stem pieces of *Fuchsia* root readily in the moist humus that is usually found in thickets where most species of the genus occur. Large colonies of *F. boliviana* that reproduce mainly in this manner were seen in Venezuela (naturalized) and in Bolivia (native). The same process also gives rise in other species to dense thickets of plants that probably arose from a single individual. In 1979 I returned to the precise locality of a hybrid between *F. gehrigeri* and *F. nigricans* that had first been collected in 1958 and found what was most probably the same population. Regrowth from viable hybrid seed cannot be discounted, but the uniformity of the population and the large number of vigorous, young shoots make it more likely that vegetative reproduction has maintained this colony for over 20 years.

DISPERSAL

Fuchsia is the only genus of Onagraceae with fleshy fruits, clearly an advanced character within the family. The berries are plump and generally reddish at maturity, with a high sugar content, and are clearly adapted to dispersal by birds.

Berries are well suited for long distance dispersal, and the distribution of widely disjunct species such as *F. cyrtandroides* on Tahiti and *F. triphylla* on Hispaniola have been explained by internal transport by birds (Carlquist, 1967). A similar long-distance dispersal event has been postulated for the early establishment of the Mexican and Central American sections of the genus. On a local scale, bird dispersal is an effective means of spreading seeds to new habitats, and it probably has been instrumental in the extension of many species into different structural units of the Andes.

CYTOLOGY

Compared with those of other Onagraceae, the chromosomes of *Fuchsia* are relatively large and unspecialized, contract evenly in the course of mitosis, and show poor differentiation into heterochromatic and euchromatic portions (Kurabayashi et al., 1962). Translocation systems common in the tribe Onagreae and aneuploidy prevalent in Lopezieae and in *Clarkia* are not found in *Fuchsia,* which retains the basic chromosome number of the family, $x = 11$.

Reports of chromosome numbers in the native species of *Fuchsia* previous to the beginning of the present study in 1977 were mostly diploid ($n = 11$), except for two tetraploid species in sect. *Quelusia, Fuchsia lycioides* (sect. *Kierschlegeria*), and a single individual of sect. *Encliandra* (Warth, 1925; Haque, 1952; Chaudhuri, 1956; Beuzenberg & Hair, 1959; Kurabayashi et al., 1962; Huynh, 1965; Breedlove, 1969). The chromosome numbers of only three of the 61 species now recognized in sect. *Fuchsia* had been reported, all diploid, but since vouchers apparently were not preserved, these reports are of little value. Recent studies conducted at the Missouri Botanical Garden have shown sect. *Quelusia* (eight spp., Brazil and the southern Andes) to be polyploid, with three tetraploid and one octoploid species known; tetraploid species have been found in the Andean sect. *Hemsleyella* (P. Berry and T. P. Ramamoorthy, unpublished). Because these sections are considered to be rather closely related to sect. *Fuchsia,* an extensive survey was undertaken in sect. *Fuchsia* to determine if polyploidy had played any significant role in the broad diversification of this section.

Methods. Gametic counts were obtained from pollen mother cells in young, field collected buds fixed in 3 parts absolute ethanol : 1 part glacial acetic acid for 24 hours; buds were then transferred to 70% ethanol. Anthers were squashed and stained in aceto-carmine or in lacto-propionic orcein. Somatic chromosome counts were obtained from actively growing root tips pretreated for 2–4 hours in 8-hydroxyquinoline, then fixed as above in acetic alcohol for 10 min. to 6 hr. The roots were hydrolyzed in 1 N HCl for 20 min. at 60°C and stained for 12–24 hr. in aceto-carmine or lacto-propionic orcein; they were then squashed and heated in equal parts glycerine and 45% acetic acid.

Results. One hundred new counts were obtained for populations of *Fuchsia*

TABLE 4. Chromosome numbers in *Fuchsia* sect. *Fuchsia*.[1]

Taxon	*n*	2*n*	Collection Data or Reference
F. abrupta I. M. Johnston	11		PERU, JUNÍN: 58 km E of Satipo, *B3078* (MO)
	11		PERU, HUÁNUCO: above Chinchao, *Mathias & Taylor 4033* (RSA)[2]
F. ampliata Benth.	11		ECUADOR, IMBABURA: 8 km W of Laguna Cuicocha, *B3169* (MO)
	11		ECUADOR, PICHINCHA: 9 km W of Chillogallo, *B3234* (MO)
F. cf. *andrei* I. M. Johnston	11		PERU, AMAZONAS: 42 km of E of Pedro Ruiz, *B3628* (MO)
F. austromontana I. M. Johnston	11	22	PERU, CUZCO: 8 km E of Abra de Acanaco, *B2594* (MO)
	11	22	PERU, CUZCO: 58 km from Ollantaytambo to Quillabamba, *B3035* (MO)
F. ayavacensis Humboldt, Bonpland & Kunth	11		PERU, PIURA: 35 km E of Canchaque, *B3630* (MO)
F. boliviana Carrière	11		COLOMBIA, ANTIOQUIA: Alto de Minas, *Escobar 1000* (MO)
	11		COLOMBIA, TOLIMA: 29 km W of Fresno, *B3552* (MO)
	11		MEXICO, CHIAPAS: Chamula, *Breedlove 8018* (DS)
	11		PERU, CUZCO: Urubamba, *B2561* (MO)
	11		PERU, APURIMAC: Ampuy, *Stork, Horton & Vargas 10595* (UC)[2]
	11		PERU, HUÁNUCO: 5 km SE of Carpish, *Stock & Horton 9921* (UC)[2]
F. canescens Benth.	11		COLOMBIA, CAUCA: 31 km E of Totoró, *B3578* (MO)
	11		COLOMBIA, CAUCA: 34 km E of Totoró, *B3579* (MO)
F. caucana P. Berry	11		COLOMBIA, NARIÑO: 24 km E of Pasto, *B3252* (MO)
F. ceracea P. Berry	11		PERU, HUÁNUCO: 5 km W of Carpish pass, *B3081* (MO)
F. cinerea P. Berry	11		ECUADOR, CARCHI: Tufiño, *B3147* (MO)
F. corollata Benth.	22		ECUADOR, CARCHI: ridge between Tulcán and El Carmelo, *B3159* (MO)
	22		ECUADOR, IMBABURA: Hacienda Curubí, *B3173* (MO)
	22		EUCADOR, IMBABURA: 11 km SW of Otavalo to Mojanda, *B3175* (MO)
	11		COLOMBIA, CAUCA: 11 km E of Totoró, *B3575* (MO)
	11		COLOMBIA, CAUCA: 4 km W of Gabriel López, *B3576* (MO)
F. corollata × ?*caucana* (probable hybrid)	22	44	COLOMBIA, CAUCA: 23 km E of Puracé, *B3584* (MO)
F. corymbiflora Ruiz & Pavón	11		PERU, HUÁNUCO: Carpish, *B3082* (MO)
F. crassistipula P. Berry	11		COLOMBIA, TOLIMA: 40 km W of Fresno, *B3553* (MO)
F. denticulata Ruiz & Pavón	11		BOLIVIA, LA PAZ: road to Chulumani, *Albert de Escobar 1305* (TEX)
	11		PERU, CUZCO: ca. 70 km from Quillabamba to Ollantaytambo, *B2573* (MO)
	11	22	PERU, CUZCO: 72 km from Quillabamba to Ollantaytambo, *B3042* (MO)
		22	PERU, CUZCO: ca. 65 km from Quillabamba to Ollantaytambo, *B3048* (MO)
		22	PERU, AYACUCHO: 41 km E of Tambo, *B3050* (MO)
F. aff. *denticulata* Ruiz & Pavón	11		PERU, CUZCO: Km 131 of Cuzco-Paucartambo-Pilcopata road, *B2598* (MO)

TABLE 4. Continued.

Taxon	*n*	2*n*	Collection Data or Reference
F. dependens Hook.	11		COLOMBIA, NARIÑO: 13 km S of Pasto, *B3145* (PSO)
	11		ECUADOR, CARCHI: 4 km W of El Carmelo, *B3164* (MO)
F. ferreyrae P. Berry	11		PERU, JUNÍN: 68 km W of Satipo, *B3073* (MO)
F. fontinalis J. F. Macbr.	11		PERU, AMAZONAS: 62 km from Balsas to Leimebamba, *B3608* (MO)
F. gehrigeri Munz	11		VENEZUELA, MÉRIDA: 43 km W of El Águila to Piñango, *B3138* (MO)
	11		VENEZUELA, MÉRIDA: 9 km above Santo Domingo to Apartaderos, *B3139* (MO)
	11		VENEZUELA, MÉRIDA: Km 19–20 from Apartaderos to Santo Domingo, *B3599* (MO)
	11		VENEZUELA, TÁCHIRA: 6 km E of Zumbador to Queniquea, *B3297* (MO)
F. gehrigeri × *nigricans*	11		VENEZUELA, TRUJILLO: Visún, above Las Mesitas, *B3129* (MO)
F. gehrigeri × *?venusta*	11		VENEZUELA, TÁCHIRA: 3.5 km E of Zumbador, *B3414* (MO)
F. hartwegii Benth.	c.11		COLOMBIA, PUTUMAYO: W of Sibundoy, *B3255* (PSO)
	11		COLOMBIA, VALLE: above El Guayabo, Palmira to Taco, *B3568* (MO)
	11		COLOMBIA, CAUCA: 21 km E of Piendamó, *B3572* (MO)
F. hirtella Humboldt, Bonpland & Kunth	c.11		COLOMBIA, CUNDINAMARCA: 23 km from Pacho to Zipaquirá, *B3538* (COL)
	11		COLOMBIA, CUNDINAMARCA: Km 34 of old Bogotá-Fusagasugá road, *B3543* (MO)
	11		COLOMBIA, CUNDINAMARCA: Km 36 of old Bogotá-Fusagasugá road, *B3543-B* (no voucher)
F. hirtella × *venusta*	11		COLOMBIA, CUNDINAMARCA: Km 39 of old Bogotá-Fusagasugá road, *B3547* (MO)
F. lehmannii Munz	11		ECUADOR, ZAMORA-CHINCHIPE: 27 km E of Loja, *B3200* (MO)
	11		ECUADOR, ZAMORA-CHINCHIPE: below El Retorno, *Mathias & Taylor 5200* (RSA)[2]
F. loxensis Humboldt, Bonpland, & Kunth	11		ECUADOR, AZUAY: above Sayausí, *B3185* (MO)
	11		ECUADOR, LOJA: 5 km S of Saraguro, *B3192* (MO)
	11		ECUADOR, PICHINCHA: Panamerican Hway S of Quito, *B3233* (MO)
F. macrophylla I. M. Johnston	11		PERU, AYACUCHO: 58 km E of Tambo, *B3053* (MO)
F. magdalenae Munz		44	(Wright, 1978a) Cultivated plants from COLOMBIA, SE slopes Sierra Nevada de Santa Marta, Trombachuca Valley, *Wright* (RDG)[3]
F. mathewsii J. F. Macbr.	11		PERU, CAJAMARCA: 39 km W of Celendín to Cajamarca, *B3602* (MO)
	11		PERU, AMAZONAS: 42 km E of Balsas to Leimebamba, *B3603* (MO)
	11		PERU, AMAZONAS: 51 km E of Balsas to Leimebamba, *B3606* (MO)
	11		PERU, AMAZONAS: 24 km above Leimebamba to Balsas, *B3612* (MO)
F. nigricans Linden	11		VENEZUELA, TRUJILLO: Agua Negra, 8 km SW of El Batatal, *B3093* (MO)
	11		VENEZUELA, TRUJILLO: 9 km SW of El Batatal, *B3095* (MO)

TABLE 4. Continued.

Taxon	*n*	2*n*	Collection Data or Reference
		c.22	VENEZUELA, TRUJILLO: 12 km from San Rafael to Trujillo, *B3104* (MO)
		22	VENEZUELA, MÉRIDA: above La Mucuy, *Berry in 1980* (MO)
	11		VENEZUELA, MÉRIDA: La Carbonera, *B3451* (MO)
F. nigricans × *venusta*	11		VENEZUELA, MÉRIDA: between La Azulita and La Carbonera, *B3453* (MO)
F. orientalis P. Berry	11		ECUADOR, ZAMORA-CHINCHIPE: 24 km E of Loja, *B3199* (MO)
	11		ECUADOR, NAPO: 10 km from Baeza to Cosanga, *B3246* (MO)
F. pallescens Diels	11		COLOMBIA, CAUCA: Km 41 W of Uribe, *B3570* (MO)
F. petiolaris Humboldt, Bonpland & Kunth	11		COLOMBIA, NORTE DE SANTANDER: 7 km above Pamplona to Bucaramanga, *B3533* (MO)
	11		COLOMBIA, CUNDINAMARCA: Cerro El Tablazo, *B3539* (MO)
	11		COLOMBIA, CUNDINAMARCA: E slopes Páramo de Choachí, *B3542* (MO)
	11		COLOMBIA, TOLIMA: 47 km W of Fresno, *B3558* (MO)
	11		COLOMBIA, TOLIMA: 48 km W of Fresno, *B3559* (MO)
F. pilosa Fielding & Gardner	11		PERU, AMAZONAS: 9 km E of Molinopampa to Mendoza, *B3618* (MO)
F. polyantha Killip	11		ECUADOR, CARCHI: 55 km W of Tulcán to Maldonado, *B3154* (MO)
F. pringsheimii Urban	22		DOMINICAN REPUBLIC, LA VEGA: Valle Nuevo, *B3707* (MO)
	c.22		DOMINICAN REPUBLIC, LA VEGA: Valle Nuevo, *B3709* (MO)
F. rivularis J. F. Macbr.	11		PERU, AMAZONAS: 9 km E of Molinopampa to Mendoza, *B3617* (MO)
F. sanctae-rosae Kuntze	11		BOLIVIA, LA PAZ: Chulumani, *Albert de Escobar 1303* (TEX)
	11		PERU (Huynh, 1965)
F. sessilifolia Benth.	c.11		ECUADOR, CARCHI: El Carmelo, *B3163* (MO)
	11		COLOMBIA, HUILA: Km 25 from Pitalito to Mocoa, *B3592* (MO)
F. sylvatica Benth.	11		ECUADOR, IMBABURA: 25 km W of Laguna Cuicocha, *B3171* (MO)
	11		ECUADOR, PICHINCHA: 25 km W of Chillogallo to Chiriboga, *B3237* (MO)
F. tincta I. M. Johnston	11		PERU, CUZCO: Km 131 of Cuzco-Paucartambo-Pilcopata road, *B2597* (MO)
	11		Source unknown, cultivated at Berkeley, California, *49.823* (UC)[2]
F. triphylla L.	22	44	DOMINICAN REPUBLIC, LA VEGA: El Convento, 10 km S of Constanza, *B3701* (MO)
	22		DOMINICAN REPUBLIC, LA VEGA: ca. 1 km above El Convento, *B3702* (MO)
F. vargasiana Munz	11		PERU, CUZCO: Km 132 of Cuzco-Paucartambo-Pilcopata road, *B3000* (MO)
F. venusta Humboldt, Bonpland & Kunth	11		VENEZUELA, MÉRIDA: El Paramito, above La Carbonera, *B3450* (MO)
	11		COLOMBIA, CUNDINAMARCA: below Zipacón, *B3540* (MO)
	c.11		COLOMBIA, CUNDINAMARCA: Km 39 of old Bogotá-Fusagasugá road, *B3548* (MO)

TABLE 4. Continued.

Taxon	*n*	2*n*	Collection Data or Reference
F. verrucosa Hartweg	22		VENEZUELA, TÁCHIRA: 6 km E of Zumbador to Queniquea, *B3417* (MO)
	c.20–22		COLOMBIA, CUNDINAMARCA: Km 34–35 to old Bogotá-Fusagasugá road, *B3535* (MO)
	22		VENEZUELA, TÁCHIRA: 5 km E of Las Porqueras to Pregonero, *B3662* (MO)
F. vulcanica André	22		ECUADOR, AZUAY: 13 km from Cuenca above Sayausí, *B3184* (MO)
		44	ECUADOR, AZUAY: 17 km from Cuenca above Sayausí, *B3187* (MO)
	22		ECUADOR, AZUAY: 18 km from Cuenca above Sayausí, *B3188* (MO)
		44	ECUADOR, AZUAY: 8 km S of Cumbe, *B3190* (MO)
	c.22		ECUADOR, NAPO: Papallacta, *B3245* (MO)
F. wurdackii Munz	11		PERU, AMAZONAS: vicinity of Leimebamba, *Hutchison & Wright 4888* (UC)[2]

[1] Numbers preceded by B were collected by the author.

[2] Counted by P. H. Raven from cultivated progeny.

[3] A separate count of $2n = 44$ was obtained by Ching-I Peng from seeds sent to the Missouri Botanical Garden by J. O. Wright.

(see Table 4), comprising 43 species and five probable hybrids. Of these, 37 species yielded only diploid counts, five only tetraploid counts, and one species both diploid and tetraploid counts. *Fuchsia vulcanica* yielded four tetraploid counts and one possible diploid count. One of the putative hybrids, *Berry 3584* (MO), is tetraploid, forming 22 bivalents at metaphase I, and appears to be an allotetraploid derived from diploid populations of *F. corollata* and *F. caucana*. Four other hybrids were diploid and had normal meiotic pairing of 11 bivalents at metaphase I, although chromosomal bridges and fragments were observed in some cells at anaphase I. Since only limited field collected material was available for the hybrids, these results should be considered tentative and their interpretation doubtful.

Two of the six tetraploid or partly tetraploid species in sect. *Fuchsia* are disjunct and confined to the island of Hispaniola. One of these, *F. pringsheimii*, has nectaries and flowers uncharacteristic for sect. *Fuchsia*; its affinities are unclear, but it may share a common ancestor with *F. triphylla*, which is also endemic to Hispaniola but much more similar to other species of sect. *Fuchsia*. Of the South American species, *F. verrucosa* and *F. magdalenae* are also considered anomalous in sect. *Fuchsia*, because of their non-annular nectaries, as well as the extremely short floral tubes in *F. verrucosa*. The only species really typical of the main body of Andean species that are tetraploid are *F. vulcanica* and *F. corollata*. These are the only two of all the tetraploid species in the section that commonly have a large, though variable, proportion of triporate pollen grains. The other four species have entirely biporate grains, as do the other diploid species in the section. In the context of other polyploids that have been studied in the family Onagraceae (P. H. Raven, pers. comm.), this suggests that *F. vulcanica* and *F. corollata* might have become tetraploid recently, and that the other

four tetraploid species may be of more remote origin and have become stabilized. In *F. corollata*, both diploid and tetraploid populations are known, and the tetraploidy doubtless originated within the species. All species in sect. *Quelusia* and the single species of sect. *Kierschlegeria* are polyploid and have entirely triporate (or rarely four-porate) grains.

SYMPATRY AND INTERSPECIFIC HYBRIDIZATION

The evaluation of sympatry and interspecific hybridization in sect. *Fuchsia* is hampered by our still fragmentary knowledge of the population structure and distribution of many species. Despite many months of field studies and over 20,000 km of road travel in the Andes, I was not able to find living plants of 12 of the rarer species in the section. The broad latitudinal distribution of the section, the enormous stretches of cloud forest on the eastern slopes of the Andes that are virtually inaccessible, and the heavy rains that often cut off areas that do have roads are all factors that contribute to the difficulty of making field observations. The amount of known sympatry (discussed for each species in the systematic treatment) and of known or suspected interspecific hybridization (presented in Fig. 17) is therefore a conservative indication of the amount that likely occurs in nature.

Figure 17 shows that evidence for interspecific hybridization was found in 23, or just over a third, of the species in sect. *Fuchsia*, and species such as *F. nigricans* and *F. sanctae-rosae* were found to hybridize with three or four different species. Evidence for individual hybrid plants is discussed under the suspected parent species in the systematic treatment except for the example of *F. nigricans* in the following discussion. The main criterion used for recognizing naturally occurring hybrids was morphological intermediacy between the presumed parents, but decreased pollen stainability and local ecological factors such as habitat disturbance and the sympatric occurrence of the parental species were also considered to be correlated with hybrid origin in many cases. Pollen viability was estimated using the double staining malachite green/acid fuchsin/orange G stain of Alexander (1969), and stainability was found to be usually 90–100% in most species of *Fuchsia*. In interspecific hybrids it is usually considerably lower, but some suspected hybrids were almost fully fertile, while others were plants that had totally aborted pollen grains. Normal meiotic pairing was observed in several hybrids, and the sterility observed is not thought to be related to chromosomal reorganization. In most cases, however, morphological intermediacy and pollen stainability of less than 70% are considered strong evidence of hybrid origin. These criteria obviously limit the recognition of most hybrids to F_1's, since backcross individuals are much harder to detect.

Although it is usually much easier to recognize living hybrid plants than dried ones, a number of hybrids were recognized from herbarium specimens, especially between morphologically well differentiated species. Because of low pollen stainability and the presence of unmistakable features of two distinct species, the type specimen of *Fuchsia caracasensis* (Fielding & Gardner, 1844) was recognized as a hybrid between *F. nigricans* and *F. gehrigeri*, both of which are known to grow near the type locality. *Fuchsia colombiana* (Munz, 1946) and *F. platypetala* (Johnston, 1939) were also probably based on hybrid individuals.

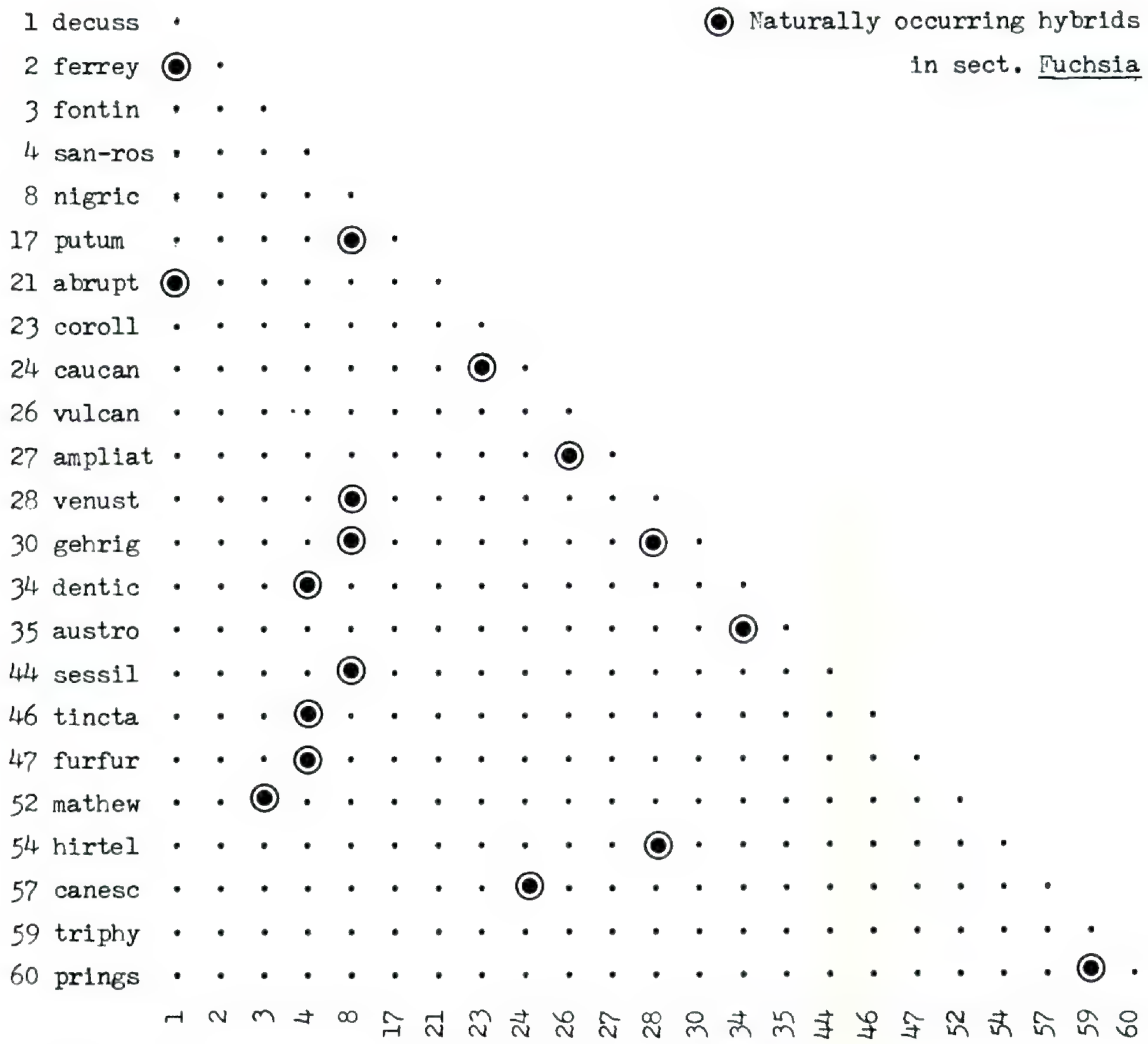


FIGURE 17. Naturally occurring hybrids in *Fuchsia* sect. *Fuchsia*.

Most hybrids found in the field were rare and localized, and the parental populations were usually large and at least partly sympatric. Hybrids between *F. triphylla* and *F. pringsheimii*, *F. venusta* and *F. hirtella*, and *F. venusta* and *F. gehrigeri* occur in a narrow belt where the different altitudinal limits of the species coincide (Figs. 5 and 6). Although human disturbance such as that associated with road cuts usually creates more local habitats for *Fuchsia* and thus increases the possibility for hybridization, hybrids of *F. venusta* and *F. gehrigeri* were also found in primary forest.

A high incidence of natural hybridization is expected in sect. *Fuchsia* for several reasons. First, the species of sect. *Fuchsia* are modally outcrossing and hummingbird-pollinated. Second, there is a high degree of sympatry between species, but remarkably little ecological differentiation. For example, *F. cuatrecasasii*, *F. scabriuscula*, *F. sessilifolia*, and *F. verrucosa* were all found growing together in the same thicket south of Pitalito on the border of Depts. Huila and Cauca, Colombia, in July 1979. Finally, the thousands of hybrids artificially produced in the 19th and 20th centuries attest to the ease of hybridization in the

TABLE 5. Floral characters of *Fuchsia nigricans*. *F. venusta*, and a presumed hybrid.

	F. nigricans (*Berry 3454*)	Hybrid (*Berry 3453*)	*F. venusta* (*Berry 3455*)
Inflorescence	Subracemose to racemes 20 cm long	Subracemose to racemes 12 cm long	Subracemose
Pedicel length	3–5 mm	9–18 mm	25–28 mm
Ovary length	10–11 mm	9–13 mm	7–9 mm
Floral tube length	19–21 mm	30–37 mm	50–60 mm
Floral tube color	Lavender pink	Red pink	Orange red
Sepal length	8 mm	14–16 mm	16–18 mm
Petal length	8–10 mm	15–17 mm	18–20 mm
Petal color	Dark purple	Medium purple	Orange red
Fruit length	19–20 mm	14–15 mm	ca. 12 mm

genus (see Porcher, 1858; Hemsley, 1876; and Reiter, 1941). Although most of these hybrids were from other sections in the genus, *F. dominiana* (van Houtte, 1854) was an early hybrid between *F. macrostigma* and *F. denticulata*. Towards the end of the 19th century, the tetraploid *F. triphylla* was used in many interspecific crosses (Wright, 1978b).

Numerous sympatric populations have been found with no evidence of hybridization, however. For example, a dense patch of *F. pringsheimii* was found growing along the edge of a potato field with scattered plants of *F. triphylla* at La Nuez, on the border of La Vega and Peravia Provinces, Dominican Republic, in December 1979. Despite the large sympatric populations and the fact that both of these species form hybrids on other parts of the island, no intermediates between these two distinctive species could be found. Only *F. triphylla* was flowering at the time, and it is possible that *F. pringsheimii* has a different flowering period at this locality. *Fuchsia tincta* and *F. vargasiana* are apparently closely related diploid species that occur side by side and flower together in southern Peru, yet no intermediate plants were detected. The same situation occurs with *F. macrophylla* and *F. macropetala* in central Peru. It is possible that hybrids between these species do occur but are not easily recognizable or were not flowering at the time the populations were examined. On the other hand, there may be prezygotic isolation mechanisms such as pollinator discrimination, especially in instances in which the sympatric species differ widely in flower size, but these are factors that have yet to be examined.

Despite the rarity of most hybrids, extensive hybrid populations were observed in two combinations. Suspected hybrids between *Fuchsia corollata* and *F. caucana* are numerous and widespread in southern Colombia. They occur in geographically intermediate areas between observed populations of the presumed parents, but at higher altitudes and in harsh subpáramo habitats. One of the probable hybrids was tetraploid. This indicates the possibility of well established hybrid populations that have occupied a new habitat and that might have originated as allotetraploids. A second case concerns probable hybrid swarms of *F. ampliata* and *F. vulcanica* in Prov. Cotopaxi, Ecuador. Very variable local populations have been found in heavily disturbed roadside areas, and these outnumber the presumed parental populations.

TABLE 6. Pollen stainability of putative hybrids of *Fuchsia nigricans* and representatives of sympatric parental populations.

Collection	Stainability
F. nigricans (*Berry 3454*)	81.8% (500 grains)
Hybrid (*Berry 3453*)	34.0% (500 grains)
F. venusta (*Berry 3455*)	81.0% (500 grains)
F. nigricans (*Bernardi 653*)	81.6% (1000 grains)
Hybrid (*Bernardi 652*)	28.5% (1000 grains)
F. cf. *venusta* (*Bernardi 664*)	69.0% (1000 grains)
Other hybrids *F. nigricans* × *F. venusta*	
Ricardi & Hernandez 5722	4.0% (500 grains)
Bernardi s.n.	less than 10%[1]
F. gehrigeri (*Berry 3128*)	88.3% (600 grains)
Hybrids × *F. nigricans*:	
Berry 3129	5.3% (300 grains)
Aristeguieta & Medina 3670	8.6% (500 grains)
Linden 368 (OXF)	21.3% (400 grains)
F. nigricans (*Fosberg & Core 21550*)	84.0% (500 grains)
Hybrid (*Fosberg 21556*)	28.6% (500 grains)
Hybrid (*Fosberg 21558*)	0.2% (1000 grains)
F. sessilifolia (*Fosberg 21560*)	94.7% (1000 grains)
F. nigricans × *F. putumayensis*:	
Robinson 138	0.6% (500 grains)

[1] Estimated due to poor stain differentiation.

The relative rarity of most hybrids found indicates that unless large or numerous populations are carefully examined, many hybrids will be overlooked, and thus that the likelihood of finding hybrid individuals is strongly dependent on the sampling intensity. The Venezuelan Andes was the only area that was intensively studied. Four species are sympatric there, *F. gehrigeri*, *F. nigricans*, *F. venusta*, and *F. verrucosa*, and all possible hybrid combinations were found except those involving *F. verrucosa*. Since this is the only tetraploid species in the group and is distantly related to the others, it is probable that postzygotic barriers to hybridization exist between *F. verrucosa* and its sympatric congeners.

Fuchsia nigricans possesses several distinctive characters such as purple petals, canescent pubescence, and elongate, tapered ovaries. Because of these features, hybrids involving this species are relatively easy to detect. These features, together with characters such as the sympatric occurrence of the parent species, field observations in some cases, and reduced pollen stainability (Table 6), were used to compile the following list and discussion of putative hybrids with this species.

Putative hybrids involving *Fuchsia nigricans*

Fuchsia nigricans × *F. venusta*. *Berry 3453* (MO, VEN): Venezuela, Edo. Mérida, Dpto. Campo Elias, 4 km below San Eusebio on the road to La Azulita, wet roadbanks, 4 April 1979. The morphologically intermediate characters of this

TABLE 7. Comparison of morphological characters in *Fuchsia nigricans*, *F. gehrigeri*, and presumed hybrids.

	F. gehrigeri (*Berry 3128*)	Hybrid (*Berry 3129*)	Hybrid (*Aristeguieta & Medina 3670*)	*F. nigricans* (Average Values)
Stem pubescence	Subglabrous to strigillose	Densely canescent to strigillose	Canescent	Densely canescent
number of secondary veins	5–7	10–12	13	12–16
Leaves/node	3–4	2–3	3	3
Pedicel length	25–35 mm	9–12 mm	8–15 mm	3–10 mm
Floral tube length	51–54 mm	30–33 mm	30–35 mm	14–22 mm
Petal length	14–15 mm	10–12 mm	13–14 mm	5–10 mm
Petal color	Red	Purple	Dark red	Dark purple
Stigma exsertion above anthers	9–10 mm	2 mm	9 mm	0–2 mm
Fruit shape	Subglobose	Cylindrical	—	Cylindrical
Seed size (L × W)	2–2.5 × 1.2 mm	1.5–2 × 1 mm (mostly aborted)	—	1.5 × 0.8 mm

collection are shown in Table 5 and in Figure 33, and the reduction in pollen stainability is evident in Table 6. Both parental species occurred side by side at this locality in wet roadside thickets (Fig. 4), though *F. nigricans* was locally more abundant. The hybrid showed strong vegetative growth and was also intermediate in pubescence and leaf texture. Meiotic preparations from *Berry 3453* had normal formation of 11 bivalents, as did samples from the parental species nearby.

Bernardi 652 (NY): Venezuela, Edo. Mérida, Monte Zerpa, cloud forest, 2,300 m, 21 June 1953. Both parental species were collected in the vicinity by the same collector on the same date, and *Bernardi 652* has flowers like *F. nigricans* except for a longer (35 mm) floral tube and mostly elliptic leaves like *F. venusta*.

Other specimens with hybrid characters similar to those described above and with low pollen fertility include *Bernardi s.n.* (NY; Venezuela, without locality, 15 Feb. 1957), *Bernardi 6119* (MER; Venezuela, Edo. Mérida, Selva La Vagabunda), and *Ricardi & Hernández 5772* (MER; Venezuela, Edo. Mérida, Valle Grande, 2,300–2,500 m).

Fuchsia nigricans × *F. gehrigeri*. *Aristeguieta & Medina 3670* (NY, VEN): Venezuela, Edo. Trujillo, Dpto. Boconó, Visún, south of Las Mesitas, ca. 2,400 m, Aug. 1958. *Berry 3129* (MO, VEN) was collected at the same site in Sept. 1978. These collections probably come from the same population, which formed a dense thicket about 5 m^2 in a sunny hollow with extensive vegetative reproduction occurring by stem shoots. Just 10 m away, several plants of *F. gehrigeri* were growing in shade along the forest edge. No plants of *F. nigricans* were seen in the vicinity, but they undoubtedly occur in the area.

The presumed hybrids are clearly morphologically intermediate between the indicated species (Table 7), and their pollen stainability is in both cases less than 10% (Table 6). Buds of *Berry 3129* were examined cytologically and had 11 bivalents at metaphase I, with occasional bridges and fragments at anaphase I. Though ripe fruits were produced in *Berry 3129*, most of the seeds were aborted.

TABLE 8. Comparison of morphological characters in *Fuchsia nigricans*, *F. sessilifolia*, and presumed hybrids.

	F. nigricans (*Fosberg & Core 21550*)	Hybrid (*Fosberg 21556*)	Hybrid (*Fosberg 21588*)	*F. sessilifolia* (*Fosberg 21560*)
Leaves/node	2–3	3–4	3–4	4
Leaf shape	Broadly elliptic-obovate	Oblanceolate-ob-ovate	Elliptic	Narrowly elliptic-lanceolate
Blade length (max.)	9.5 cm	15 cm	13 cm	18 cm
Petiole length	15–20 mm	8–10 mm	6–15 mm	5–11 mm
Leaf margin	Subentire to den-ticulate	Serrulate	Denticulate	Serrate to serrulate
number of secondary veins	10–11	17–18	13–16	15–19
Floral tube color	Dull crimson	Green red to crimson	Crimson	Green
Petal color	Dark purple	Crimson to pur-ple	Purple	Red
Inflorescence	Spreading, race-mose	Drooping, pani-culate	Drooping, sub-paniculate	Drooping, panicu-late

Two other probable hybrids with *F. gehrigeri* are *Benítez de Rojas 1887* (VEN; Venezuela, Edo. Trujillo, road from Boconó to Trujillo) and *Linden 368* at OXF (OXF; Venezuela, Edo. Mérida, between Mendoza and Timotes, 1843). This latter collection was used as the type specimen of *F. caracasensis* Fielding & Gardner (Sert. Pl. *t. 29.* 1844) but has highly inviable pollen (Table 6) and a series of intermediate characters between *F. nigricans* and *F. gehrigeri* such as long floral tubes, elongate ovaries, unequal leaf bases, and oblong leaves. The same collection number at P was used to describe *F. nigricans,* but this and the duplicates at BM, G, K, LE, TCD, US, and W are clearly different, with high pollen stainability and no indication of intergradation with *F. gehrigeri.*

Fuchsia nigricans × *F. sessilifolia. Fosberg 21556* (RSA, US): Colombia, Chocó, 7 km N of Carmen de Atrato, bank above trail, 2,675 m, 6 March 1944, "calyx varying from greenish red to crimson, corolla from crimson to purple." Also *Fosberg 21558* (RSA, US): 8 km N of Carmen de Atrato, steep bank above trail, same date, "calyx crimson, corolla purple, with *21560* (= *F. sessilifolia*) but colors not intergrading." Both of these collections have highly reduced pollen stainability and characters clearly intermediate between *F. nigricans* and *F. sessilifolia* (Tables 6 and 8). The variability and intermediate flower color noted above is also indicative of their hybrid origin. *Fuchsia nigricans* was collected along the same trail at 2,500 m, and *F. sessilifolia* grew together with *Fosberg 21588.* Although the flower size and shape of the two parental species are very similar, the very different leaves and flower color offer excellent indicators for analyzing presumed hybrids. The combination of such distinctive characters as the subsessile, lanceolate leaves of *F. sessilifolia* and the purple petals of *F. nigricans* leave little doubt as to the parentage of the presumed hybrids.

The largely triporate pollen grains found in *Fosberg & Core 21550* (*F. nigricans*) are noteworthy. The four diploid counts of *F. nigricans* from Venezuela were made from plants with biporate grains. Triporate grains in *Fuchsia* are sometimes indicators of polyploidy, so there may be tetraploid populations of this taxon in Colombia. If so, this would perhaps explain the extremely low pollen stainability of the presumed hybrids between these rather closely related species.

Fuchsia nigricans × *F. putumayensis*. *Robinson 138* (COL, K, US): Colombia, Dept. Valle, Río Bravo, northwest of Darién, 4,200 ft., 28 July 1962. This plant has almost entirely inviable pollen (Table 6). The purple petals and elongate ovaries indicate genetic input from *F. nigricans*. The subnitid, sulcate-nerved upper leaf surface is typical of *F. putumayensis*, however, as are the divergent, slender petals. The rachis is too long for that species, though, and the leaves are often ternate as in *F. nigricans*. Both presumed parent species have been collected in the general area, and the low altitude indicated on Robinson's label is consistent with the parentage of *F. putumayensis*, which grows at lower altitudes (from ca. 1,200–1,800 m) than any other species in the Cordillera Occidental of Colombia.

All of the preceding evidence supports a high degree of interfertility in most species of sect. *Fuchsia* and indicates that natural interspecific hybridization is a common, but not ubiquitous, phenomenon between sympatric species. When hybrids do occur, they are usually rare and localized, but two examples were given that illustrate the evolutionary potential of populations of hybrid origin that have become better adapted to certain habitats than the parent species. The increased genetic recombination afforded by interspecific hybridization has probably been of considerable adaptive significance in sect. *Fuchsia* during the late Tertiary uplift of the Andes and especially in the Pleistocene, when new and disturbed habitats were formed as a result of severe climatic fluctuations.

THE EVOLUTION OF *FUCHSIA* SECT. *FUCHSIA*

One of the main questions addressed by this study is how and why so many more species evolved in *Fuchsia* sect. *Fuchsia* than in other sections of the genus. Through the evidence presented in the preceding sections, it is possible to attempt answers to this question.

We can begin by distinguishing the importance of extrinsic or physical factors from ones related to the plants themselves. Prior to the Neogene, the tropical Andes were probably too low for fuchsias to occur there. In the context of angiosperm evolution, the Andes are newly uplifted mountains, and they are furthermore composed of a number of distinct structural units. Starting in the Miocene, and especially during the Pliocene, they were strongly uplifted from the surrounding lowland tropical areas to give rise to a wide variety of new habitats over a very broad geographical area. Cool, montane forest habitats ("cloud forest" or "Andean forest") first appeared and increased in extension, followed by open, high elevation habitats ("puna" and "páramo"). In this way, large expanses of new, cool habitats in the tropics became available for adaptation by lowland, tropical taxa, or for colonization by previously cool-adapted organisms

from temperate areas. The latter possibility was shown to be the case in *Fuchsia*, which had a probable Paleogene origin in temperate South America.

The other key extrinsic factor in understanding plant evolution in the Andes is the series of strong climatic changes that occurred as a result of Pleistocene glaciations, whose magnitude in the tropics went largely unrecognized until the last two decades. As discussed in Raven (1980), drastic climatic shifts (such as those caused by the uplift of the Andes and by Pleistocene glaciations) produce new or fundamentally altered environments, thereby setting the stage for rapid speciation. This can also be described as an increase in the ecological opportunity for the establishment of new immigrants or new adaptive gene combinations (Mayr, 1963).

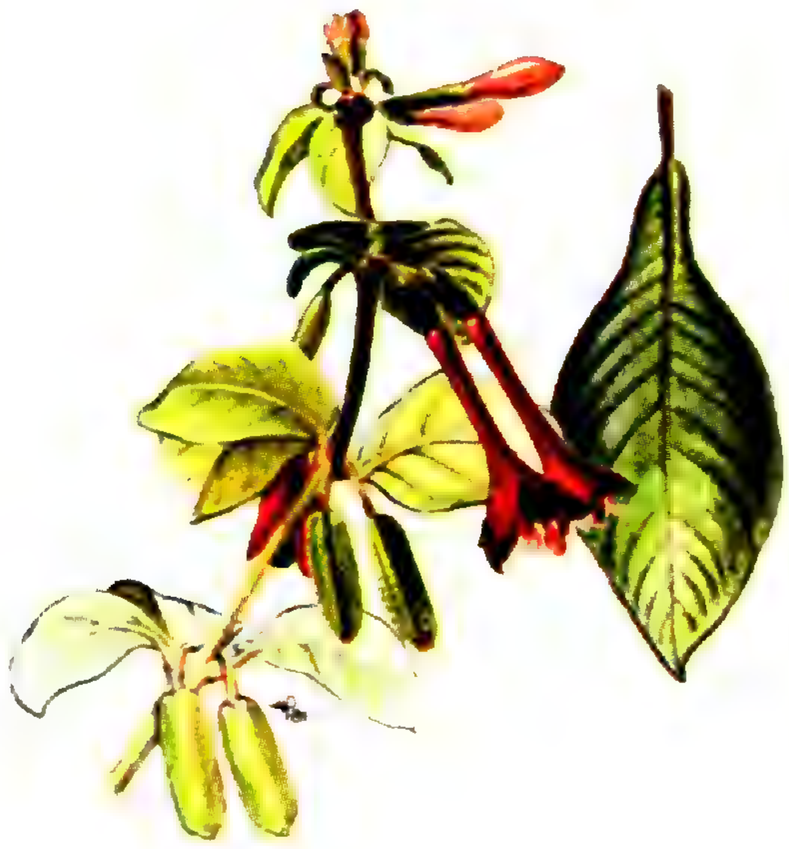
The ways to exploit and adapt to these changes in the physical conditions of the Andes are seen in the different reproductive strategies that the organisms inhabiting them have evolved. *Fuchsia* is a good colonizer as a result of its self-compatibility and dispersal by birds. This is probably how the genus migrated into the tropical Andes and reached isolated islands such as Tahiti and Hispaniola. Especially when new Andean forest habitats were developing, major jumps within the tropical Andes may have occurred by long-distance dispersal. Populations established in this way may have formed the nuclei of the different species groups that we recognize today, and which are usually centered in a specific geographic area. Bird dispersal is an important factor in local migrations as well, such as those discussed previously between the different structural units of the Andes.

Certain ecological adaptations were favorable to the diversification of sect. *Fuchsia* in the Andes. Of the two sections of the genus now present in the tropical Andes, sect. *Hemsleyella* became adapted to seasonal conditions and developed a basically epiphytic or lithophytic habit, whereas sect. *Fuchsia* is more generalized and remains more or less aseasonal in mesic, terrestrial habitats. Section *Fuchsia* has over four times as many species as sect. *Hemsleyella* over roughly the same geographical range.

Because members of sect. *Fuchsia* are restricted to mesic habitats where more or less constant moisture is available, they have not radiated strongly into different ecological zones. Nonetheless, many species have become adapted to different altitudinal tolerances and can remain spatially isolated on the same mountain range. Montane cloud forests are dynamic communities where natural disturbances such as landslides, tree falls, clearings, and water courses abound. These are the main areas where sect. *Fuchsia* occurs, though man-made disturbances have recently added a new dimension to this system. The particularly flexible breeding system of sect. *Fuchsia* is well adapted to such disturbed habitats; plants are loosely growing, mostly scandent shrubs that are modally outcrossing but self-compatible and have a relatively high and constant flowering rate, yet they are capable of considerable vegetative reproduction. These are adaptations that would have been particularly advantageous during the Pleistocene, when habitat disturbances were increased by the glacial cycles.

Adaptation to hummingbird pollination has been another important factor in the evolution of sect. *Fuchsia*. Hummingbirds can maintain their flower-visiting activity throughout the year in cool, wet habitats whereas insects are far more

FIGURES 18–19. Illustrations of *Fuchsia* sect. *Fuchsia*.—18 (Left). *Fuchsia crassistipula* P. Berry, from *Berry 3553* (MO), Tolima, Colombia. Scale: floral tubes of open flowers are 46 mm long.—19 (Right). *Fuchsia denticulata* Ruiz & Pavón, from *Berry & Aronson 3048* (MO), Cuzco, Peru. Scale: floral tube of the open flower is 43 mm long.



FIGURES 20–22. Illustrations of *Fuchsia* sect. *Fuchsia*.—20 (Upper half). *Fuchsia abrupta* I. M. Johnston, from *Berry & Aronson 3077* (MO), Junín, Peru. Scale: floral tubes of largest open flowers are 45 mm long.—21 (Lower left). *Fuchsia nigricans* Linden, from *Berry 3095* (MO), Trujillo, Venezuela. Scale: floral tubes of open flowers are 20 mm long.—22 (Lower right). *Fuchsia scabriuscula* Benth., from *Berry & Escobar 3178* (MO), Pichincha, Ecuador. Scale: floral tubes of open flowers are 23 mm long.

limited in their activity. Like *Fuchsia,* hummingbirds have diversified mainly in the tropical Andes. Although the dynamics of hummingbird pollination in *Fuchsia* have not been examined, it is likely that at least in some species the differences in floral tube length restrict interspecific pollination by hummingbirds.

Enough cytological data is now available to state that sect. *Fuchsia* is chromosomally homogeneous, and species tend to be largely interfertile. Six species are tetraploid or partly so, but these occur mostly in outlying geographical areas or have morphological features anomalous in the section. The presence of numerous naturally occurring hybrids, the near normal meiotic behavior of those hybrids examined, and the existence of at least two cases of widespread populations of probable hybrid origin, indicate that interspecific hybridization on the homoploid level, rather than polyploidy, has probably played an important role in the evolution of the section.

It is now recognized that the lack of internal barriers to hybridization in plants, especially in perennials, is more the rule than the exception, and that the main differences between plant groups occur in the nature and strength of external mechanisms that restrict interspecific hybridization (Raven, 1980). In other groups in the Onagraceae that have radiated very recently, such as *Epilobium* in New Zealand (Raven & Raven, 1976) and *Oenothera* in South America (Dietrich, 1978), interspecific hybridization has been the key feature in the differentiation of new taxa, but the different units now recognized as species have remained distinct mostly through predominant autogamy, strong radiation into widely different habitats, and the unique genetic system of complex structural heterozygotes in the case of *Oenothera*. *Fuchsia* sect. *Fuchsia,* on the other hand, has not been able to radiate much beyond the cloud forest zone, and it is primarily outcrossing, with specialized hummingbird pollination, rather than autogamous. Other cloud forest groups such as *Monochaetum* (Almeda, 1978) have reproductive systems similar to *Fuchsia,* and these are likely to prove quite common in other groups of woody Andean angiosperms.

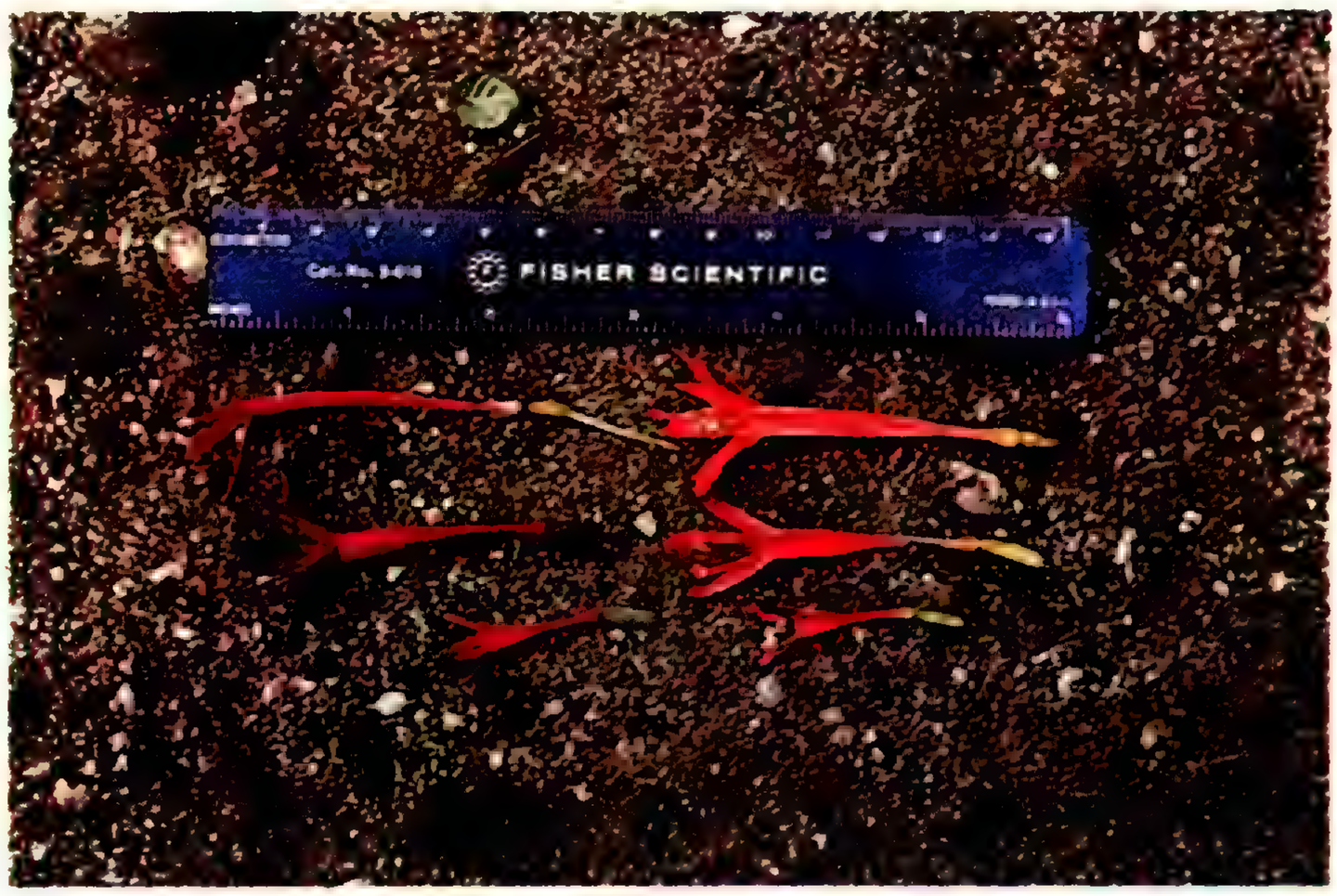
INTERSPECIFIC RELATIONSHIPS IN *FUCHSIA* SECT. *FUCHSIA*

The lack of any major morphological, cytological, or ecological differentiation in all but a few of the 61 species in sect. *Fuchsia* precludes a formal division of the species into series or other subsectional taxonomic categories. The mode of evolution in sect. *Fuchsia* appears to have been strongly reticulate, permitting only clusters of rather closely related species to be recognized. In general, it has not been possible to discriminate between more primitive or advanced species, and this may in part be due to the recent differentiation of the section.

Munz (1943) informally divided sect. *Fuchsia* into two lines, species with long floral tubes and those with short floral tubes. Groups were circumscribed based on inflorescence structure. The shape of petals and floral tubes was used to further subdivide the species. Because a continuous range of floral tube lengths from 3 to 130 mm exists in the species of sect. *Fuchsia,* it is arbitrary to divide them into two groups on this basis. Pairs of closely related species are known, such as *F. polyantha* and *F. sessilifolia,* in which one species is short-tubed and the other long-tubed.

FIGURES 23–26. Illustrations of *Fuchsia* sect. *Fuchsia*.—23 (Upper left). *Fuchsia ampliata* Benth., from *Berry & Escobar 3234* (MO), Pichincha, Ecuador. Scale: floral tube of open flower is 45 mm long.—24 (Upper right). *Fuchsia venusta* Humboldt, Bonpland & Kunth, from *Berry 3292* (MO), Táchira, Venezuela. Scale: floral tubes of open flowers are 48 mm long.—25 (Lower left). *Fuchsia harlingii* Munz, from *Berry & Escobar 3206* (MO), Loja, Ecuador. Scale: floral tubes of open flowers are 48 mm long.—26 (Lower right). *Fuchsia caucana* P. Berry, from *Berry 3590* (MO), Huila, Colombia. Scale: floral tube of open flower is 40 mm long.

FIGURES 27–30. Illustrations of *Fuchsia* sect. *Fuchsia*.—27 (Upper left). *Fuchsia ferreyrae* P. Berry, from *Berry & Aronson 3073* (MO), Junín, Peru. Scale: floral tubes of open flowers are 26 mm long.—28 (Upper right). *Fuchsia verrucosa* Hartweg, from *Berry 3286* (MO), Táchira, Venezuela. Scale: ovary is 11 mm long.—29 (Lower left). *Fuchsia triphylla* L., from *Berry, Smith & Mejía 3701* (MO), La Vega, Dominican Republic. Scale: floral tube of open, lowermost flower is 36 mm long.—30 (Lower right). *Fuchsia pringsheimii* Urban, *Berry, Smith & Mejía 3711* (MO), La Vega, Dominican Republic. Scale: floral tubes are 27 mm long.



FIGURES 31–33. Illustration and photographs of *Fuchsia* sect. *Fuchsia*.—31 (Left). *Fuchsia ceracea* P. Berry, from *Berry & Aronson 3081* (MO), Huánuco, Peru. Scale: sepals of the left hand flower are 29 mm long. Note the tender, concave bracts sheathing the base of the flowers.—32 (Upper right). The hummingbird *Chlorostilbon swainsonii* visiting *Fuchsia triphylla*. Both species are endemic to Hispaniola. Photograph by Donald Dod, taken between Constanza and Valle Nuevo, Prov. La Vega, Dominican Republic.—33 (Lower right). Flowers of two sympatric species of sect. *Fuchsia* and their hybrid. Upper flower is from *F. venusta* (*Berry 3455*, MO), the lower flower is from *F. nigricans* (*Berry 3454*, MO), and the middle flower (*Berry 3453*, MO) is from a natural hybrid between the above species. Note the intermediate size and color of the hybrid flowers. The three plants were found growing together in roadside thickets between La Carbonera and La Azulita, at 2,200 m, Edo. Mérida, Venezuela, in June 1979; their habitat is illustrated in Figure 4, and further evidence of the probable hybrid origin of *Berry 3453* is given in the text.

Whereas my key to the species of sect. *Fuchsia* closely follows Munz's scheme, a different approach has been used here to recognize species groups. Floral position, tube length, and petal shape are used here, but these characters were analyzed in more detail and were supplemented by ecological, geographical, cytological, and vegetative characters. Instead of a dichotomous, linear system, 14 different species groups that are intended to reflect the evolutionary relationships between the species more realistically are proposed. These species groups are first approximations and should not be regarded as formal taxonomic categories.

The order of the species groups is not necessarily meant to reflect any particular evolutionary sequence, though the short-tubed, axillary-flowered species may be more primitive and are placed at the beginning. Those species of doubtful affinity are included with the closest probable species group, and those of unknown affinities are placed together in a final group. Each species group is followed by a brief summary of its principal characteristics.

1) *Fuchsia decussata* species group: *F. decussata, F. ferreyrae, F. fontinalis,* and *F. sanctae-rosae* (Fig. 55). Short-tubed, mostly axillary flowers with narrow petals. The first three are closely related and have divaricate or predominantly horizontal branching and denticulate leaves, but *F. fontinalis* has flowers tending towards a paniculate inflorescence. *Fuchsia sanctae-rosae* has thicker, less constricted floral tubes, nearly entire leaves, more erect branching and is more distantly related to the first three species. Peru and Bolivia.

2) *Fuchsia loxensis* species group: *F. loxensis, F. scabriuscula, F. steyermarkii* (Fig. 56). A very loosely connected group with exclusively axillary flowers, short to medium floral tubes, and rather broad petals. *Fuchsia loxensis* is treated as a polymorphic species whose taxonomy is not fully understood; its round petals and large leaves suggest that it may be close to the *F. petiolaris* species group. *Fuchsia scabriuscula* has no clear relative and has very few flowers and opposite, reticulate leaves, unlike the other members of this group. The linear leaves of *F. steyermarkii* are unique in the section, but its flowers resemble those of *F. loxensis* more than any other species. Colombia and Ecuador.

3) *Fuchsia nigricans* species group: *F. nigricans, F. sylvatica, F. pallescens, F. orientalis,* and *F. glaberrima* (Fig. 57). Characterized by mostly short-tubed, axillary to racemose flowers with narrow petals, short pedicels, and cylindrical ovaries and fruits. The first three species are closely allied and each has petals that are considerably darker than the sepals. The transitional stages of axillary to racemose inflorescences are particularly evident in these species. The last two species are closely related and have definite racemes with persistent bracts and prominent stipules, but the flowers and leaves of *F. orientalis* link the two subgroups together. Venezuela to northern Peru.

4) *Fuchsia macrophylla* species group: *F. macrophylla, F. macropetala, F. ovalis,* and *F. pilosa* (Fig. 56). The first two species are closely related and, with *F. ovalis,* have lateral or axillary inflorescences rather than the usual terminal or subterminal ones (Fig. 40). Though *F. pilosa* has a terminal inflorescence, it is

placed here because of the close similarity of leaves, flowers, and pubescence to *F. ovalis*. Short-tubed, except for *F. macropetala*. Peru.

5) *Fuchsia putumayensis* species group: *F. putumayensis, F. lehmannii, F. andrei, F. cuatrecasasii,* and *F. abrupta* (Fig. 58). Short to long floral tubes with reddish orange flowers, and delicate, usually recurved petals. Flowers mostly densely packed in short, terminal racemes with lanceolate, recurved, or deciduous bracts. Pedicels usually divergent. *Fuchsia abrupta* is long-tubed and has elongate inflorescences; its affinities are unclear, but it is placed here because of its strongly divergent pedicels, delicate, recurved petals, and mostly opposite leaves, which are found in most of the above species. Colombia to central Peru.

6) *Fuchsia petiolaris* species group: *F. petiolaris, F. corollata, F. caucana, F. ayavacensis, F. vulcanica,* and *F. ampliata* (Fig. 59). Long-tubed, axillary flowers with various shaped, often pubescent petals. High altitude, often subpáramo habitats. A well delimited group, but individual species are similar and poorly defined. Populations of *F. vulcanica* and *F. corollata* are tetraploid. Additional cytological and population sampling is needed, especially for *F. vulcanica, F. corollata,* and *F. petiolaris*. Southernmost Venezuela to northern Peru.

7) *Fuchsia venusta* species group: *F. venusta, F. rivularis, F. gehrigeri, F. llewelynii, F. scherffiana,* and *F. confertifolia* (Fig. 60). Medium- to long-tubed flowers with narrow petals, in the upper axils or in incipient racemes with mostly long pedicels. The first two species are closely related and have a common climbing habit, crispate petals, subcoriaceous elliptic leaves, and slightly hairy petals. They are probably linked to the *F. petiolaris* species group through *F. gehrigeri*. Since the last three species are known only from a few fragmentary collections, their affinities are unclear. *Fuchsia confertifolia* has very distinctive reduced leaves, but they are subcoriaceous as in the first two species, and the more or less crispate petals and axillary to racemose inflorescence place it closest to this group. *Fuchsia llewelynii* and *F. scherffiana* are probably closely allied and are placed here on the basis of their subcoriaceous leaves, long pedicels, and medium-long flowers. Venezuela to northern Peru.

8) *Fuchsia denticulata* species group: *F. denticulata, F. austromontana, F. harlingii, F. cochabambana, F. macrostigma,* and *F. magdalenae* (Fig. 61). Long-tubed, axillary flowers with thick, firm, mostly cylindric floral tubes. Pedicels stout; petals variable, but often drying purplish; anthers large (3–6 mm long). A distinctive group in its solitary, stout flowers. The first three species are closely related. *Fuchsia cochabambana* has funnelform flowers grouped at the tips of branches, but they are more or less thick-tubed and have purple-drying petals as in the first two species. *Fuchsia macrostigma* has thick, axillary flowers, but long, curved, narrowly funnelform floral tubes with large, spreading petals and a massive quadrangular stigma. Though *F. magdalenae* seems clearly to belong to this group because of its strong resemblance to *F. denticulata,* it has an entirely different type of nectary from the rest of the species in sect. *Fuchsia*. It is also tetraploid and isolated on the Sierra Nevada de Santa Marta range. Colombia to Bolivia.

9) *Fuchsia simplicicaulis* species group: *F. simplicicaulis*, *F. ceracea*, *F. coriacifolia*, and *F. sanmartina* (Fig. 62). Very rare, viny shrubs with long to very long floral tubes and petals generally (much) shorter than the sepals. The first two species are unique in the genus with involucres of short-pedicellate flowers and thin membranous, concave, sessile bracts. The latter two species have racemose inflorescences but seem to be derived from, or at least closely related to the first two. The bracts of *F. coriacifolia* are smaller than those of the first two species, but they are still sessile and slightly concave; the basal flowers of the inflorescence are verticillate; the upper flowers are alternate. The inflorescences of *F. sanmartina* have mostly alternate flowers, and the bracts are lanceolate, short-petiolate, and mostly deciduous. Central Peru.

10) *Fuchsia sessilifolia* species group: *F. sessilifolia* and *F. polyantha* (Fig. 63). Two closely related species, one with short, bicolored flowers and the second with long, uniformly red flowers. Leaves quaternate, lanceolate, subsessile, nitid dark green. Flowers in well-branched terminal panicles. Colombia and Ecuador. *Fuchsia sessilifolia* shares several important characters with the *F. nigricans* species group.

11) *Fuchsia tincta* species group: *F. tincta*, *F. furfuracea*, and *F. vargasiana* (Fig. 62). A closely related group with opposite, ovate leaves and pilose pubescence; short, few-flowered, terminal, corymbiform racemes with long pedicels. Endemic to southern Peru and Bolivia.

12) *Fuchsia boliviana* species group: *F. boliviana*, *F. corymbiflora*, *F. wurdackii*, and *F. mathewsii* (Figs. 63 and 65). A loosely united group with large, pubescent leaves and terminal, long racemes or few-branched panicles of long-tubed flowers. *Fuchsia boliviana* is distinctive in its arborescent habit, wide ecological tolerances, reflexed sepals, and early petal dehiscence. The leaves of these species are mostly opposite or ternate, which distinguishes them from the following group. Northern Peru to northern Argentina (excluding the naturalized range of *F. boliviana*).

13) *Fuchsia dependens* species group: *F. dependens*, *F. hirtella*, *F. hartwegii*, *F. crassistipula*, *F. canescens*, and *F. cinerea* (Fig. 66). Pubescent, mostly quaternate leaves, narrow petals, flowers mostly paniculate and long-tubed. The first three species are very closely related, differing mainly in tube and petiole length. *Fuchsia crassistipula* is also allied to these species but has unusually thick, persistent stipules and frequently more than four leaves per whorl. *Fuchsia canescens* has thick floral tubes and intermediate axillary to racemose flowers. Though the flowers of *F. cinerea* are all axillary, the leaves and individual flowers are very similar to *F. dependens*, and it cannot be placed in any other species group. Colombia and Ecuador.

14) Anomalous species: *F. triphylla*, *F. pringsheimii*, and *F. verrucosa* (Figs. 65 and 67). All three of these species are tetraploid and cannot be placed close to any of the preceding groups. Except for its disjunct distribution, low-growing habit, and suberect inflorescences, *F. triphylla* has no features in which it differs substantially from the Andean species. *Fuchsia pringsheimii*, like *F. triphylla*, is

endemic to the island of Hispaniola. It has very small leaves, broad, obconic floral tubes, and large, emarginate petals unlike any other species in sect. *Fuchsia*. It also possesses a non-annular, lobed nectary that is clearly atypical of the section. Although it does not closely resemble *F. triphylla*, the two do hybridize on Hispaniola, and they may have evolved from a distant, common ancestor.

Fuchsia verrucosa also has an atypical non-annular nectary (Figs. 46 and 47) as well as an extremely reduced floral tube. Although it occurs in Venezuela and Colombia, well within the main range of sect. *Fuchsia*, it shows no clear affinities to any of the species in that group, and, unlike all other members of sect. *Fuchsia*, it has smooth viscin threads (J. Nowicke, pers. comm.).

Morphology and Anatomy

HABIT

All species in sect. *Fuchsia* are basically perennial shrubs or lianas. Although two species, *F. pallescens* and *F. triphylla*, can flower while still remaining essentially herbaceous, woody-stemmed plants are more common. *Fuchsia boliviana* is usually arborescent and can reach a height of 6 m with a stem diameter of up to 5 cm. A number of species such as *F. glaberrima*, *F. pilosa*, *F. tincta*, *F. vargasiana*, and *F. verrucosa*, are suberect and rarely exceed a height of 2–3 m. Many others, however, can surpass this height and then become scandent or climbing. Since plants of sect. *Fuchsia* usually grow in moist thickets, they can rely on neighboring trees or brush for support. The closely related *F. dependens* and *F. hartwegii* commonly occur as semierect hedgerow shrubs in disturbed or semicultivated sites, but in suitable areas such as streamside forests, they occur as lianas clambering well into the canopy of small trees. *Fuchsia denticulata* is a widely distributed species that grows as erect shrubs in the drier parts of its range but as scandent or climbing plants in cloud forest. A few species, such as *F. venusta* and *F. rivularis*, are especially prone to climbing and often have long, flexible stems trailing along the ground until suitable support such as a tree or tangle is found (Fig. 3). They reach heights of 10–15 m by means of long, flexuous-pendant branches. One species, *F. ceracea*, is known only as a liana with long, drooping branches. A few herbarium sheets of species such as *F. petiolaris* and *F. nigricans* record their habit as epiphytic, but all plants of sect. *Fuchsia* that I examined in the field were rooted in the ground.

STEMS

Carlquist's (1975) comparative analysis of Onagraceae wood anatomy showed that species of *Fuchsia* have relatively long and wide vessel elements, as expected of mesomorphic species. Unlike most Onagraceae, however, *Fuchsia* lacks interxylary phloem. This character state is undoubtedly primitive in the family and is shared only by *Ludwigia* and *Hauya*, two other relatively unspecialized genera (Carlquist, 1975). Within the genus, sect. *Fuchsia* lacks the tuberous-thickened stems frequently found in the related sects. *Ellobium* and *Hemsleyella*.

The most useful external stem characters in sect. *Fuchsia* are the branching pattern, cross-sectional configuration, color, and bark texture on older stems.

Branching pattern. Most species are loosely branched near the base or distal to a relatively short main stem. The branches are usually ascending when young but then become spreading or drooping when they elongate and age. *Fuchsia fontinalis* and *F. ferreyrae* commonly have horizontally spreading secondary branches. The related *F. decussata* is unique in the section with its well developed branching system and short, strongly divaricate tertiary branchlets. The higher order branches of *F. confertifolia* are very much shortened and ascending. *Fuchsia scabriuscula* is often low-growing with divergent to nearly prostrate branches. Those species with a climbing habit often have a flexuous main stem and long, poorly branched secondary branches that vary from divergent to drooping or pendant. A few species such as *F. glaberrima*, *F. pilosa*, and *F. sessilifolia* generally have few or no secondary branches.

Stem cross-section. The majority of species in sect. *Fuchsia* have terete branchlets, but some have branchlets that are noticeably ridged, which can be a diagnostic field character. The upper stems of *F. crassistipula* have a series of ridges and deep furrows that correspond in number to the petioles of the whorl of leaves above it, but the ridges begin to disappear towards the basal part of the internode. Another species with conspicuously ridged stems is *F. canescens*, and a few species such as *F. venusta* lack the prominent ridges of the above species, but have trigonous or angled stems.

Stem color and bark texture. Light green or reddish stems are typical of most species of *Fuchsia*. Dull bluish purple stems are characteristic of *F. venusta*, as are smooth purple stems for *F. harlingii* and *F. rivularis*. Rusty colored stems occur at times in *F. mathewsii*, *F. decussata*, and *F. fontinalis*, as a result of their ferrugineous-pilose pubescence. Young stems of *F. verrucosa* are somewhat tuberculate, and *F. llewelynii* has numerous spinescent projections on the stems and pedicels.

Older, woody stems have three basic bark types. The most common is the sort of flaky, exfoliating bark typical of *F. decussata* and thick-stemmed species such as *F. hartwegii*, *F. gehrigeri*, *F. loxensis*, and *F. boliviana*. Also widespread is the finely fissured, grayish tan bark characteristic of *F. andrei*, *F. hirtella*, and *F. putumayensis*. Finally, a third smooth bark that splits off in a few long, wide strips occurs in *F. harlingii*, *F. rivularis*, and *F. magdalenae*.

PUBESCENCE

The few glabrous or nearly glabrous species in sect. *Fuchsia* are *F. ceracea*, *F. polyantha*, *F. putumayensis*, and *F. cuatrecasasii*. In the remaining species, the pubescence can be quite variable between populations, but it is usually constant enough to distinguish species with fundamentally different pubescence types. Trichomes in *Fuchsia* are all simple and one- to few-celled (R. Keating, pers. comm.). The basic pubescence types used in the species descriptions include *puberulent* (minute, erect hairs), *canescent* or *incanous* (dense, fine grayish white hairs), *hirsute* (erect, moderately stiff hairs ca. 1 mm long), *hispid* (stiff, erect hairs more than 1 mm long), *pilose* (soft, suberect hairs less than 1 mm long), *strigose* (± appressed hairs 0.5–1 mm long), *strigillose* (± appressed hairs less than 0.5 mm long), and *villous* (loose, soft hairs ca. 1 mm long). Additional color

or texture terms (e.g., ferrugineous, pruinose) are used to supplement the basic types described above.

LEAVES

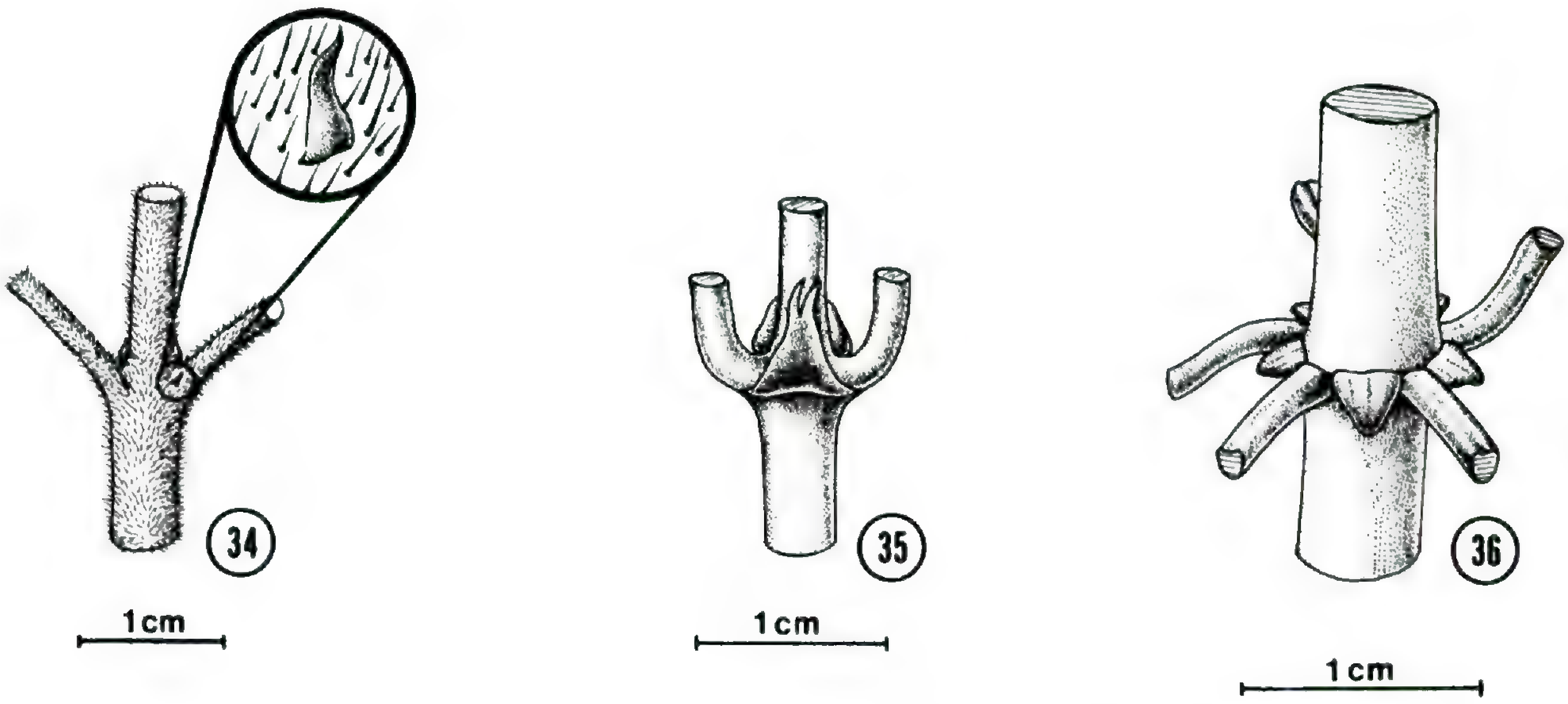
The leaves of sect. *Fuchsia* are simple, opposite or whorled, usually petiolate, stipulate, and pinnately veined. The secondary veins depart from the midvein at a right to acute angle and generally curve apically toward the margin, either joining the superadjacent secondary to form marginal loops and an intramarginal vein (brochidodromous type of Hickey, 1973) or diminishing toward the margin without forming marginal loops with the superadjacent secondary (essentially the eucamptodromous type of Hickey, 1973). The secondary veins are commonly more or less sulcate on the dorsal surface and prominent on the ventral side. The number of secondary veins is often a diagnostic leaf character, but comparison between species should be based on similar basal leaves. A diagnostic character of *F. verrucosa* is the clearly impressed brochidodromous venation. *Fuchsia steyermarkii* and *F. coriacifolia* are unusual in their almost inconspicuous secondary veins. The secondary veins of *F. caucana* have an unusually acute angle of divergence, and they remain straight until nearly the margin of the leaf. *Fuchsia scabriuscula* and some populations of *F. sylvatica* have conspicuous higher order venation that gives a rugulose-reticulate appearance to the leaf surface.

Leaf anatomy studies by R. Keating (1980, in prep.) have determined the following basic leaf structure in *Fuchsia*: one trace, unilacunar nodes; protruding midribs with a semicircular primary vasculature; blade with a thick, single-celled cuticle, single palisade and mesophyll layers; stomata present only on the ventral surface, and raphides in vertical bundles in the palisade layer. In dried specimens the raphide bundles appear to be parallel to the leaf surface.

Stipules. The stipules in sect. *Fuchsia* lose much of their diagnostic value once the plants are dried. The commonest stipule type is thin, narrowly lanceolate, not connate, and early deciduous (Fig. 34). Some species, however, have connate stipules or a mixture of separate and connate ones, making them interpetiolar and reminiscent of those of the Rubiaceae (Fig. 35). By far the most distinctive stipule type in the genus is found in *F. crassistipula*: the stipules on the lower leaf nodes are large, persistent, incrassate, connate, recurved, and with a thickened midvein (Fig. 36). Other species with thick, prominent, and persistent stipules are *F. canescens, F. glaberrima, F. orientalis, F. ovalis,* and *F. pilosa. Fuchsia abrupta* usually has large, connate stipules, but they are not thickened as in the above species. *Fuchsia wurdackii* has unusually long (3–5 mm), pale, chartaceous, blunt-tipped stipules.

Leaf margin. The margins of *Fuchsia* leaves typically have glandular, "fuchsioid" teeth (Hickey, 1980). These teeth may be inconspicuous, however, so that the margin appears entire in species such as *F. putumayensis, F. macrophylla,* and *F. cuatrecasasii.* Other species in the section are remotely to markedly denticulate or serrulate. Strongly serrulate leaves characterize *F. cochabambana* and *F. sessilifolia,* and the margins of *F. confertifolia* and *F. steyermarkii* are recurved.

General leaf characters. Mature leaves in sect. *Fuchsia* vary in length from



FIGURES 34–36. Main stipule types in *Fuchsia* sect. *Fuchsia*.—34. The most common type of separate, lanceolate stipules, *F. boliviana*, from living material growing at El Portachuelo, D.F., Venezuela.—35. Connate, interpetiolar stipules, *F. verrucosa*, *Berry 3662* (MO).—36. Incrassate, connate stipules of *F. crassistipula*, *Berry 3553* (MO).

1 to 27 cm. *Fuchsia confertifolia* has tiny, coriaceous leaves less than 15 mm long, and the leaves of *F. decussata* and *F. pringsheimii* rarely exceed 4 cm long. Species with leaves exceeding 10 cm long include *F. macrostigma*, *F. macrophylla*, *F. glaberrima*, *F. boliviana*, and *F. sessilifolia*. Leaves of most species range from 3 to 10 cm long and 1.5 to 4 cm wide and are membranous. *Fuchsia steyermarkii* is a very distinctive species with linear leaves just 3 mm wide. A few species are readily distinguishable by their nearly sessile leaves (*F. cochabambana*, *F. confertifolia*, *F. sessilifolia*, and *F. polyantha*). Ovate leaves are unusual in the section and characterize the *F. tincta* species group as well as many plants of *F. boliviana*. Unusual leaf textures are found in *F. coriacifolia* (firm-coriaceous), *F. ceracea* (waxy-pruinose), and *F. pallescens* (thin membranous). A few species are commonly found that have leaves strongly purple-flushed on the under surface. The best examples of this unusual coloration are *F. triphylla*, *F. tincta*, and *F. glaberrima*.

The number of leaves per node varies in many species, but it is quite constant in certain groups. Exclusively opposite leaves are found in *F. corymbiflora*, *F. cuatrecasasii*, *F. putumayensis*, *F. tincta*, and *F. verrucosa*. Predominantly quaternate leaves occur in the *F. dependens* and *F. sessilifolia* species groups.

INFLORESCENCES

Floral position and arrangement is one of the best diagnostic characters in sect. *Fuchsia*, and definite trends can be recognized in certain groups. The four basic types of floral arrangement in sect. *Fuchsia* are 1) axillary, 2) verticillate or involucrate, 3) racemose, and 4) paniculate (Figs. 37–41). Intermediate arrangements occur between all these types, especially between axillary and racemose flowers. The position of the inflorescence is also important; most are terminally disposed, but the *F. macrophylla* species group has distinctly axillary racemes or panicles.

Axillary flowers are considered the least advanced type, since they are the basic type found in the rest of the genus and family. Four sections of *Fuchsia* have flowers that are exclusively axillary (*Quelusia, Encliandra, Skinnera,* and *Kierschlegeria*), and only two small, probably advanced sections are exclusively racemose or paniculate (*Jimenezia* and *Schufia*). Section *Hemsleyella* is a specialized section that has axillary and racemose flowers, these last derived from axillary flowers through the shortening of the terminal internodes (Berry, unpublished). In the three species of sect. *Ellobium,* the most generalized species has axillary flowers, the intermediate one has racemose flowers, and the most advanced species has lateral panicles (Breedlove et al., 1982).

The strictly involucrate type of inflorescence (Fig. 38) is rare in sect. *Fuchsia,* found only in two species of the *F. simplicicaulis* species group. These species are unique in having sessile, concave bracts. The apparently derived *F. coriacifolia* maintains the similar sessile (but only slightly concave) bracts; its inflorescence has elongated into a raceme with the basal flowers verticillate and the distal ones alternate. In *F. simplicicaulis,* a verticillately branched system of terminally arranged involucres sometimes occurs.

Plants with axillary flowers that intergrade into terminal racemes are relatively common, especially in the *F. nigricans* species group. Rachis length is a diagnostic character in species that have inflorescences. The *F. putumayensis* species group is characterized by very short, corymbiform racemes with narrow bracts and often divergent pedicels. Species such as *F. boliviana, F. wurdackii,* and *F. pilosa* have elongate racemes.

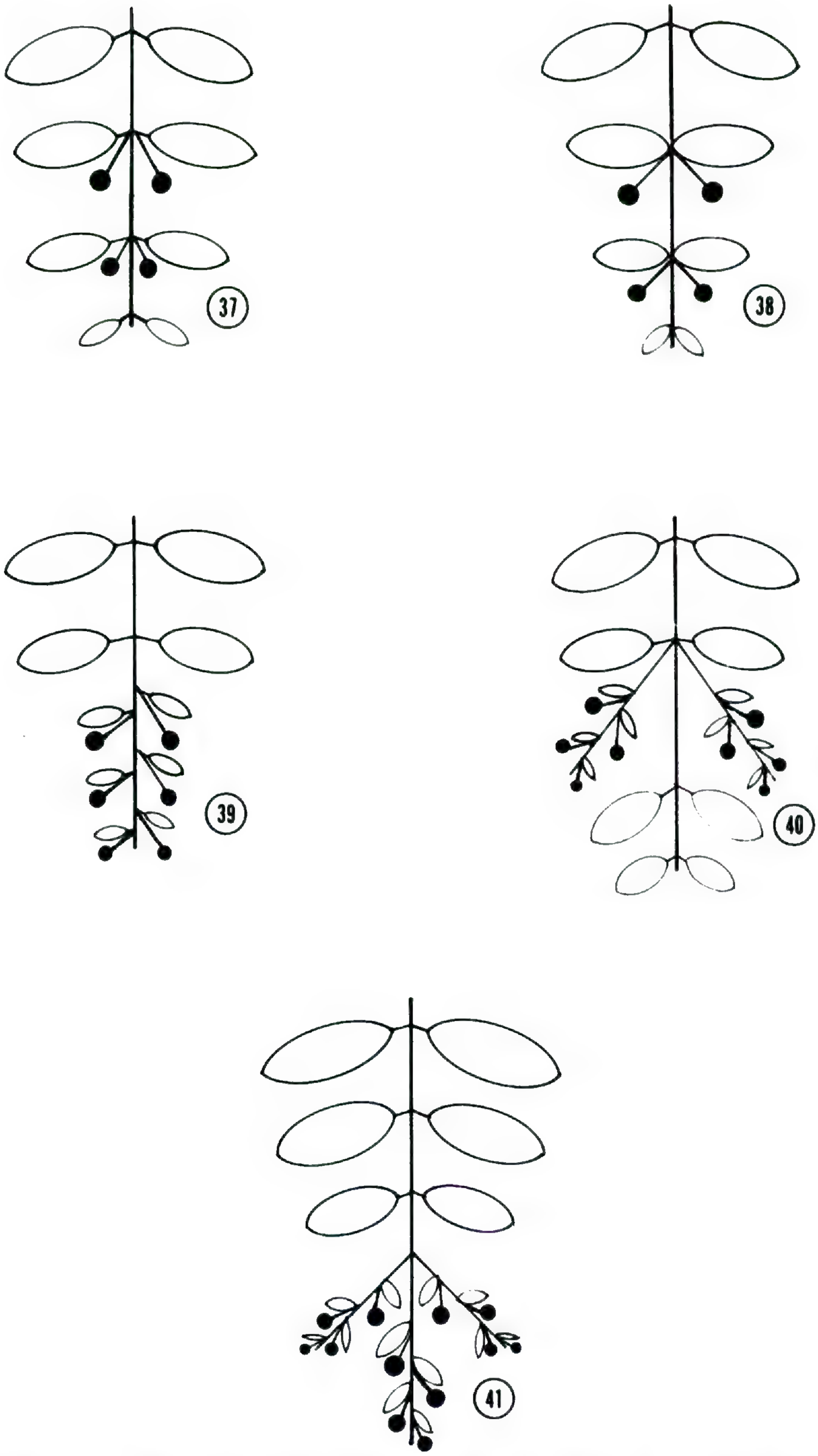
The inflorescences of the *F. dependens* and *F. sessilifolia* species groups are almost entirely paniculate, and intermediate racemose to paniculate inflorescences are found scattered in several species groups, as in *F. ovalis, F. boliviana, F. mathewsii,* and *F. fontinalis.*

FLORAL CHARACTERS

Floral tube and sepals. In all species of *Fuchsia* there is an elongate floral tube above the inferior ovary. The tube length is measured from the top of the ovary to the rim of the tube on which the sepals, petals, and stamens are inserted. The length of the floral tube in the section varies from 3 mm (*F. verrucosa*) to 130 mm (*F. ceracea*), but the length is constant within fairly narrow limits for most species and is a valuable taxonomic character.

Flowers in sect. *Fuchsia* are divergent to drooping, but never erect. Most species have floral tubes that are somewhat nodose or bulbous at the base around the nectary, creating a nectar reservoir inside the tube. This character varies with tube shape and there is little or no bulging at the base in more or less cylindric tubes such as are commonly found in the *F. denticulata* species group. On the other hand, strongly nodose floral tubes occur in *F. triphylla* and *F. ferreyrae,* both species with marked constrictions in their lower portions.

An important field character is the texture and thickness of the floral tube. Most species have tubes that are membranous and well under 1 mm thick when fresh. The *F. denticulata* species group and a few other species such as *F. canescens* and *F. coriacifolia* have firm-fleshy floral tubes with thick, spongy walls 1–2 mm thick when fresh. Thick tubes may well have evolved in connection with



FIGURES 37–41. Basic inflorescence types in *Fuchsia* sect. *Fuchsia*.—37. Axillary flowers; present in several species groups.—38. Involucrate flowers with sessile bracts; found only in the *F. simplicicaulis* species group.—39. Terminal racemes; found in several species groups.—40. Lateral racemes; found only in the *F. macrophylla* species group.—41. Terminal panicles; typical of the *F. dependens* species group.

protection against flower piercers. Tetragonous floral tubes are typical of *F. verrucosa,* and less markedly angled tubes are found in *F. pringsheimii* and part of the *F. putumayensis* species group.

The sepals are valvate in bud and generally resemble the floral tube in texture and thickness. Presence and length of sepal tips in buds varies. *Fuchsia pilosa, F. rivularis,* and *F. macrostigma* have free, spreading sepal tips in bud. At anthesis, the angle of the sepals is suberect to divergent in most species, but both *F. ampliata* and *F. boliviana* are immediately recognizable because their sepals become fully reflexed soon after anthesis.

Petals. Important petal characters are shape, size relative to the sepals, presence of pubescence, texture, surface, and angle at anthesis. Only a few species have pubescent petals, and in these cases the hairs are distributed on the outer side. *Fuchsia petiolaris* has the most consistently hairy petals, which vary from having a few villous hairs along the midnerve to having scattered or dense, puberulent hairs. Hairs can also be found on petals of some populations of *F. gehrigeri, F. harlingii, F. venusta,* and *F. rivularis.*

The petal surface of *F. boliviana, F. venusta,* and *F. rivularis* is usually ridged, and the petal margin can be somewhat undulate or crispate. The petal margins of *F. magdalenae* are often irregular in the distal half, with a small mucronate tip. *Fuchsia boliviana* is the only species that has petals that regularly dehisce before the tube drops off. Unusual petal shapes include the trullate (trowel-shaped) petals in *F. canescens,* rhomboid petals in *F. corollata,* and large, obovate, emarginate petals in *F. pringsheimii.*

Flower color. Flower color is an important field character, and species that are often difficult to distinguish with dried herbarium specimens are immediately separable in the field by their distinctive coloration patterns. Though all species have some basic red coloration, many species are characterized by orange, lavender, purple, or scarlet colors. Others have color gradations within the flower. *Fuchsia nigricans,* for example, has pinkish sepals and floral tubes but contrasting dark purple petals and filaments (Fig. 21). Several species, like *F. denticulata,* have green sepal tips (Fig. 19). This species usually has more or less orange petals that contrast with the waxy red or pink floral tube. *Fuchsia ferreyrae* has deep blue violet flowers, a color unique in the section (Fig. 27). Other distinctively colored flowers are those of *F. caucana* (purple lavender, with darker petals), *F. sessilifolia* (pale greenish floral tubes with red petals), and *F. pallescens* (pale pink floral tubes with red purple petals). In the *F. denticulata* species group, the petals characteristically dry with purple streaks that are not evident when the flowers are fresh.

Androecium. The eight stamens are all erect and biseriate, and the antesepalous filaments are always longer than the antepetalous ones. In the species descriptions, the measurements of the antesepalous filaments are always listed first, followed by the antepetalous ones.

Gynoecium. The inferior ovary is four-locular with unspecialized axile placentation (Eyde & Morgan, 1973). The numerous ovules are anatropous and biseriate in each locule. Ovaries are either terete or quadrangular in transection. Style

pubescence can vary in certain species, so it is only of relative value. Stigmas are smooth-surfaced with a wet stigmatic surface (Raven, 1979a), and they vary in shape from clavate to capitate or obconic. The stigma always separates into four lobes, but these may be very slight as in *Fuchsia denticulata*, or they may consist of 4 large, prominent mounds as in *F. macrostigma*.

Nectaries. Nectaries recently have been found to be a highly diagnostic character at the sectional level (Breedlove et al., 1982). Section *Fuchsia* is characterized by having an annular nectary that is not found in any other section. This nectary is formed by a ringlike disc that surrounds the style at the base of the tube. The ring is mostly free from the tube or attached only at its base and can usually be dissected out of the flower intact; it is entire in some species or four-, eight-, or irregularly lobed in others (Figs. 42 and 43). All other sections have nectaries that are mostly or completely fused to the floral tube. Three species in sect. *Fuchsia* have anomalous nectary types, however. *Fuchsia pringsheimii* has an irregularly lobed nectary that is fully adnate to the floral tube (Fig. 44); its flowers are anomalous in sect. *Fuchsia* in other respects, and it is isolated on the island of Hispaniola. *Fuchsia magdalenae* seems to belong to the *F. denticulata* species group based on general floral characters, but its nectary consists of a smooth or slightly ridged band adnate to the tube, similar to the nectaries in sects. *Hemsleyella* and *Ellobium* (Figs. 45 and 48). *Fuchsia verrucosa* is yet another anomalous species in sect. *Fuchsia*, and its nectary is composed of four separate, antesepalous lobes adnate to the floral tube (Figs. 46 and 47). All three of these species are tetraploid, have biporate pollen, and are distinctive from other members of the section.

FRUITS

The berries of sect. *Fuchsia* vary in shape from cylindrical-fusiform to globose. When ripe, they usually have a reddish coloration clearly related to dispersal by birds. Seeds in sect. *Fuchsia* vary approximately twofold in size and are generally of little taxonomic value. Because they number from ca. 50 to 200 per fruit, the seeds are laterally compressed and irregularly oblong-triangular in shape, with considerable variation within the same fruit. Bright red seeds, rather than the typical tan brown ones, are sometimes found in fruits of *F. caucana*, *F. scabriuscula*, and *F. sessilifolia*.

POLLEN

Onagraceae pollen is probably the most distinctive of the angiosperms, because of the viscin (exine) threads, protruding apertures, and atypical (for the dicots) structure of the exine.

The unusual ultrastructure of Onagraceae has been analyzed and documented

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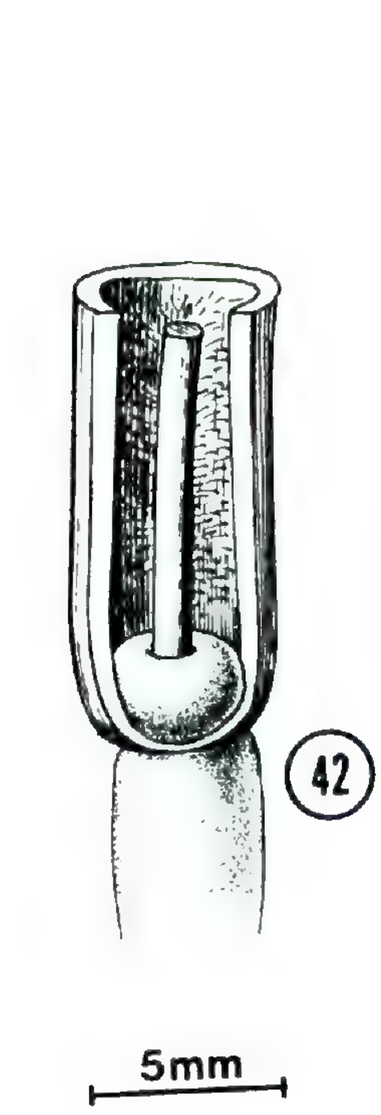
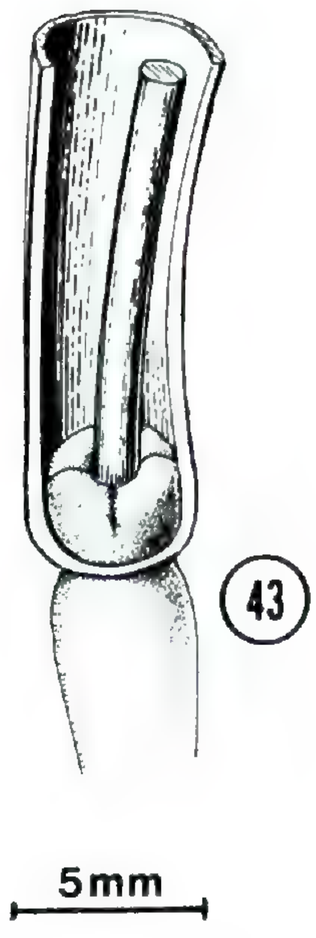
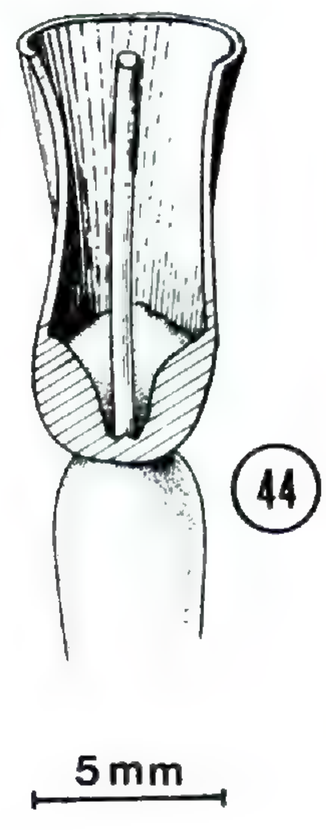
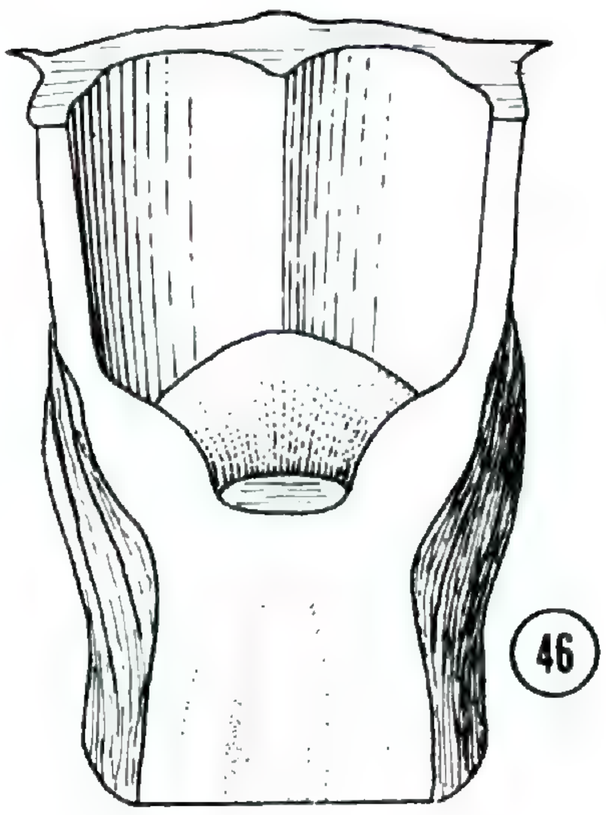
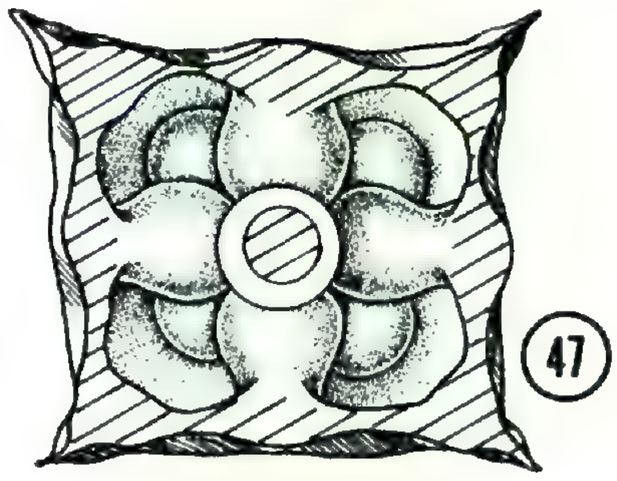
FIGURES 42–48. Nectary types in *Fuchsia* sects. *Fuchsia* and *Hemsleyella*.—42–47. Sect. *Fuchsia*.—48. Sect. *Hemsleyella*.—42–46, 48. Longitudinal sections.—47. Cross-section through the floral tube above the nectary, viewed from above.—42. Unlobed ring, *F. denticulata*, *Berry 3065* (MO).—



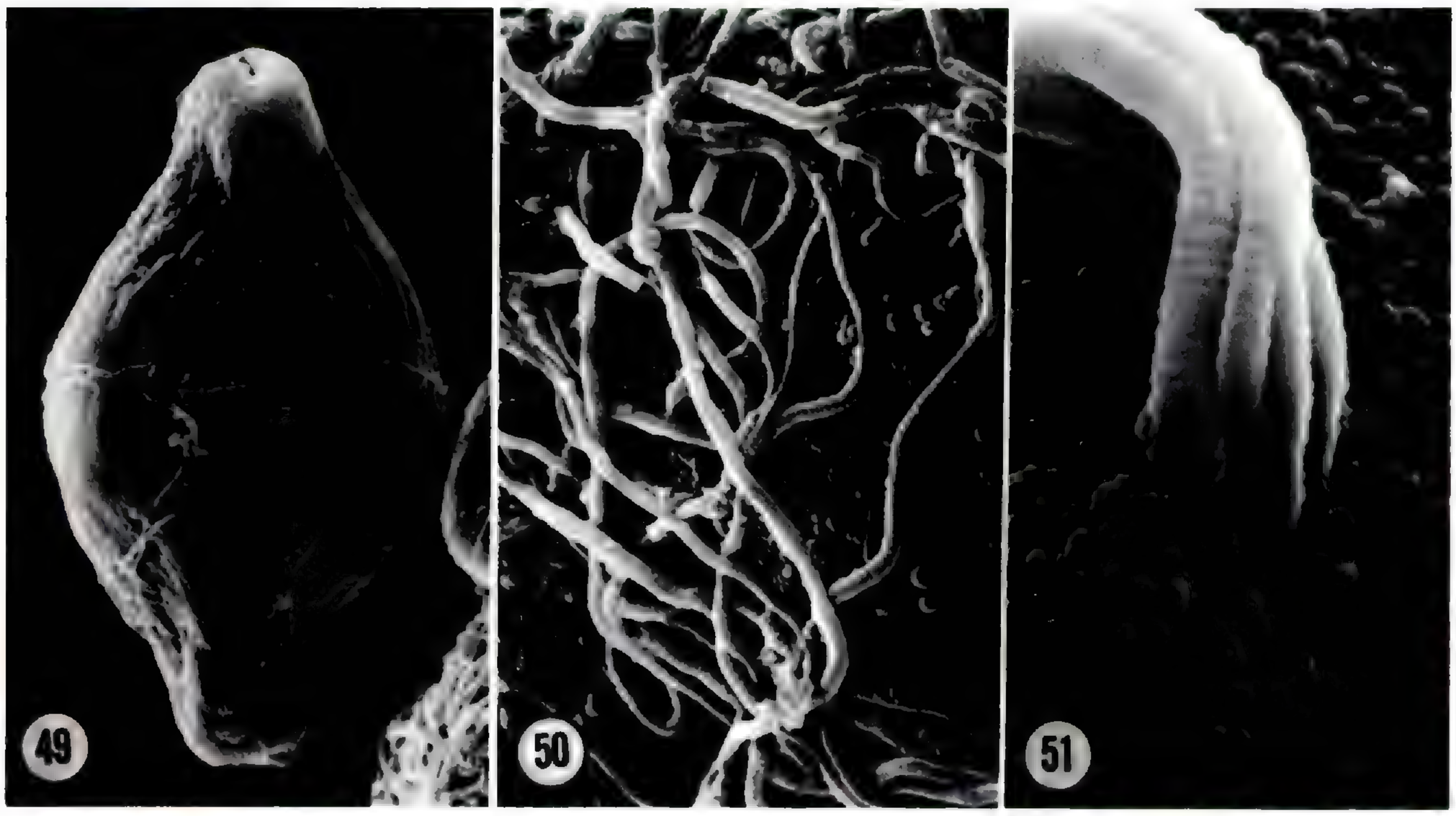








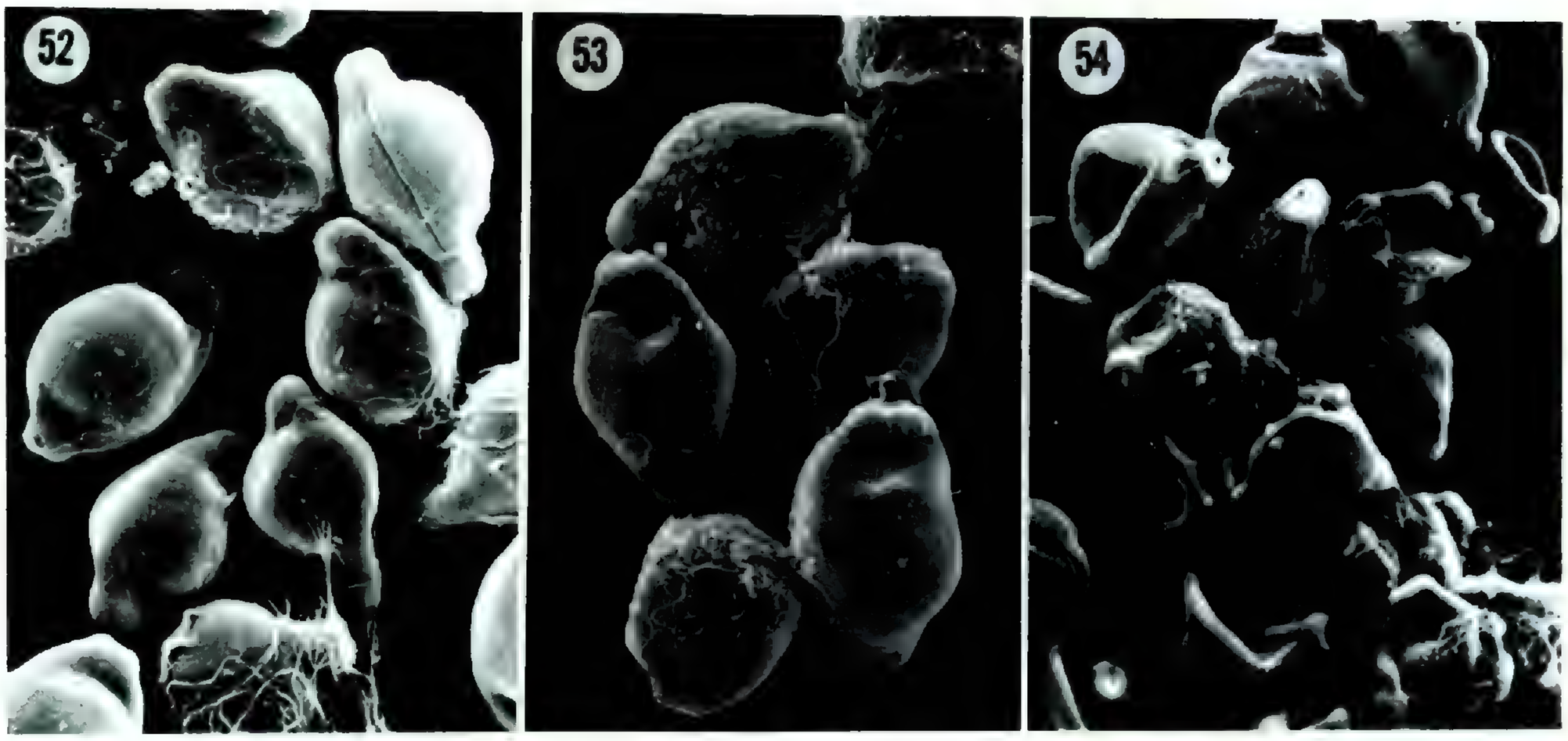
43. Four-lobed ring, *F. boliviana, Berry 2592* (MO).—44. Irregularly lobed, adnate nectary of *F. pringsheimii, Berry et al. 3709* (MO).—45. Nectary of *F. magdalenae, J. O. Wright* (pickled material, MO), consisting of nectariferous tissue lining the floral tube with 4 poorly defined prolongations. Note general similarity to the nectaries of sect. *Hemsleyella* (see Fig. 48).—46, 47. Separate, antesepalous lobes of *F. verrucosa, Berry 3662* (MO). Style removed in Figure 46.—48. Smooth band nectary lining the base of the floral tube, *F. juntasensis, Berry 3638* (MO); this type of nectary is characteristic of sects. *Hemsleyella, Ellobium,* and *Skinnera.*



FIGURES 49–51. SEM of pollen from *Fuchsia* sect. *Fuchsia*. (Provided by Joan W. Nowicke.)—40–50. *F. pilosa, Berry 3618* (MO).—49. Whole grain, equatorial view (?), ×1,550.—50. Surface of exine with viscin threads, ×5,000.—51. *F. putumayensis, Berry 3562* (MO), viscin thread attachment, ×15,000. Note beaded thread type.

in a series of publications by J. J. Skvarla and coworkers (Skvarla et al., 1975, 1976, 1978). The taxa illustrated in the nine plates by Skvarla et al. (1976) include 17 of the then recognized 18 genera and are representative of the family. In most dicotyledons, the exine is stratified and consists of an ektexine that includes tectum, columellae, and foot layer, and an endexine. In most Onagraceae pollen, however, the exine is distinctly bizonal in thin section, and consists of an external spongy layer and an internal solid one. The spongy layer is now considered to represent the ektexine and it may be more or less homogeneous as in almost all species of *Fuchsia,* or it may be coarsely granular on the proximal face, e.g., as found in *Gongylocarpus* (Skvarla et al., 1976: Plate 3F), or the ektexine may be differentiated into a tectum and columellae, with the latter being uniform in size and distribution, e.g., as in *Camissonia arenaria* (Skvarla and Nowicke, unpublished data). The inner solid layer is now considered to be the endexine and is remarkably similar in all taxa examined in thin section (Skvarla et al., 1976; Nowicke and Skvarla, pers. comm.).

In *Fuchsia* (Figs. 49–54) the mature pollen is shed in monads, the grains are paraisopolar or heteropolar, and two-aperturate and bilaterally symmetrical (Figs. 49, 52, 53) or more rarely three-aperturate and radially symmetrical (Fig. 54). They are very large, and longest dimensions of 100 μm are not uncommon. The apertures are compound and protruding, the ectoaperture is porate or slightly elliptical (elongated horizontally), the endoaperture consists of a circular oval-shaped opening in the endexine, and the massive deposition around this opening makes the endoaperture very conspicuous in light microscopy. The sculpture of the ektexine surface consists of globular elements, ovoid elements, or more rarely elongated



FIGURES 52–54. SEM of pollen from *Fuchsia* sect. *Fuchsia*. (Provided by Joan W. Nowicke.)—52. *F. putumayensis, Berry 3562* (MO), grain at center left illustrates the expanded distal pole or face, the prominent "ridge" visible on a number of grains reflects the deposition of the endexine, ×500.—53. *F. loxensis, Berry 3185* (MO), views of grains at bottom right and center left are probably that of the distal pole but grains are partially collapsed, ×500.—54. *F. vulcanica, Berry 3190* (MO), almost all grains in this micrograph are 3-aperturate, but the sample included 2-aperturate ones also, ×350.

elements. The viscin threads are mostly segmented-beaded or segmented-spiral, or more rarely smooth.

The vast majority of the Onagraceae, 590 of 675 species, have pollen with three apertures. However, in *Fuchsia*, 86 of 100 species have pollen with two apertures and in this respect the genus is unique within the family and a rarity in the dicotyledons. All species of the polyploid sections *Quelusia* and *Kierschlegeria* have three-aperturate pollen. However, the separation of two-aperturate pollen from three is by no means absolute. In sect. *Fuchsia*, known polyploid populations of *F. vulcanica* and *F. corollata* show varying proportions of two and three-aperturate pollen grains. In a sample of the polyploid species *F. pringsheimii* there were a few grains with three apertures, but the apertures were not equidistant from each other. The remaining three tetraploid species in sect. *Fuchsia, F. triphylla, F. verrucosa*, and *F. magdalenae*, were entirely two-aperturate. In addition, a number of species known only as diploids, such as *F. nigricans* and *F. venusta*, have a small proportion of three-aperturate grains (see Brown, 1967). Although increase in aperture number often accompanies polyploidy (see above for sect. *Quelusia*, and Mosquin, 1966, for *Epilobium*), and this correlation clearly applies to sect. *Fuchsia*. It has been suggested for other onagraceous genera such as *Clarkia* that the occurrence of normal pore numbers in certain polyploid species and higher numbers in other polyploid species can be associated with older vs. more recent polyploidy (P. Raven, pers. comm.)

Since a majority of the species of *Fuchsia* have segmented threads, including all of the generalized South American sections, *Fuchsia, Hemsleyella*, and *Quelusia*, as well as the early disjunct sect. *Skinnera*, this type of thread can be

TABLE 9. The distribution of viscin thread type, pollen pore number, and ploidy level in *Fuchsia*.

Section	Viscin Thread Type[1]	Pore Number	Gametic Chromosome Number
Quelusia	Compressed beaded	3	22, 44
Fuchsia	Compressed beaded	2, 3	11, 22
Hemsleyella	Compressed beaded	2, 3	11, 22
Ellobium	Compressed beaded	2	11
Kierschlegeria	Smooth	3	22
Schufia	Smooth	2	11
Jimenezia	Smooth	2	11
Encliandra	Smooth, ropy, and transitional smooth to beaded	2	11
Skinnera	Loosely beaded	2	11

[1] From Skvarla et al., 1978; Nowicke et al., in prep.

assumed to be primitive in *Fuchsia*. Smooth threads were found in the three probably derived Mexican and Central American sections, *Encliandra, Jimenezia,* and *Schufia,* as well as in the monotypic, anomalous sect. *Kierschlegeria* from coastal Chile. A general correlation found by Skvarla et al. (1978) was that segmented threads are associated with bird or moth pollination, whereas smooth, simple threads are associated with bee pollination. In *Fuchsia,* the sections with large hummingbird-pollinated flowers all have segmented threads, while all those with smooth threads have small flowers and may have at least some degree of insect pollination.

The pollen of species in sect. *Fuchsia* is remarkably similar and for that reason has limited taxonomic value. A summary of the distribution of viscin thread types, pore number, and ploidy level is presented in Table 9.

SYSTEMATIC TREATMENT

Taxonomic history of Fuchsia *sect.* Fuchsia. The earliest publication of *Fuchsia* was the description and illustration of "Fuchsia triphylla flore coccineo" by Charles Plumier in his *Plantarum Americanarum Genera* (1703). This species was found by the French missionary and naturalist during a stay in Haiti from 1689 to 1697 and was dedicated to Leonhart Fuchs, an important sixteenth century herbalist. The generic name *Fuchsia* was validated by Linnaeus (1737, 1753), using Plumier's plate as the type of *Fuchsia triphylla* L.

The first group of South American species of sect. *Fuchsia* was discovered in Peru by the Spanish explorers Hipólito Ruiz and José Pavón between 1778 and 1788. They subsequently described six new species in the section (Ruiz & Pavón, 1802). A similar surge of collections and new species resulted from the explorations of Alexander von Humboldt and Aimé Bonpland in the northern Andes from 1800 to 1802. Five new species were described from their collections in a later publication (Humboldt et al., 1823).

As a result of the great horticultural interest that fuchsias generated in Europe in the early to mid-1800s, a large number of new discoveries were made in South

America. The biggest contribution came from specimens collected by Theodor Hartweg in Colombia and Ecuador in 1841 to 1843. In a series of fascicles begun in 1839 and called *Plantae Hartwegianae*, George Bentham described 12 new species of *Fuchsia*, 8 of which are currently recognized in sect. *Fuchsia*. Andrew Mathews made a set of valuable collections from northern Peru between 1830 and 1841, but no complete sets of his collections have been maintained. Fielding and Gardner (1844) described 2 species from Mathews' collections at Oxford, and Macbride (1940) found more extensive specimens at Geneva, from which he described 3 more species. Édouard André (1888) later followed much the same route in South America as Hartweg and managed to find several more novelties in sect. *Fuchsia*.

In the 20th century, Johnston (1925, 1939) and Macbride (1940, 1941) reviewed contemporary collections, mostly of A. Weberbauer from Peru, A. S. Hitchcock from Ecuador, and Macbride's own Peruvian collections, describing between them 26 new species in sect. *Fuchsia*. Only 11 of these names are currently recognized, however, which reflects the lack of a comprehensive understanding of the group by these authors. Regional floristic treatments of sect. *Fuchsia* have been made for Peru (Macbride, 1941) and for Ecuador (Munz, 1974). Philip Munz's (1943) generic revision of *Fuchsia* was the only attempt to examine the entire genus taxonomically at a sectional and specific level. Munz described nine new species in sect. *Fuchsia*, and a total of 100 species in 7 sections were recognized in the genus. Unfortunately, Munz's inability to examine critical material from European herbaria because of the outbreak of World War II and his lack of field experience and understanding of South American geography limited the thoroughness of his work.

Since Munz's monograph, collections of sect. *Fuchsia* have been enriched by important collectors such as José Cuatrecasas, John Wurdack, Ramón Ferreyra, César Vargas, and Julian Steyermark, as well as by a large number of other botanists including the author. The result of these collections has been a better geographical coverage of the areas in which *Fuchsia* occurs and a substantial increase in the number of specimens available, which has enabled us to redefine species limits and ranges in many taxa of the genus.

Fuchsia Linnaeus, Sp. Pl. 1191. 1753. TYPE: *Fuchsia triphylla* L.

Tilco Adanson, Fam. 2:498. 1763. TYPE: *Thilco* Feuillée, J. Obs. Phys. Math. Bot. Amér. Mérid. 3:64, *pl. 47*. 1725. "Thilco" or "Chilco" is the common name in Chile for *Fuchsia magellanica* Lamarck, and there is no doubt that this is what Feuillée illustrated and described.

Skinnera J. R. & J. G. A. Forster, Charact. Gen. 57. 1771. TYPE: *S. excorticata* J. R. & J. G. A. Forster = *Fuchsia excorticata* (J. R. & J. G. A. Forster) Linnaeus f.

Quelusia Vandelli, Fl. Lusit. Brasil. 23, *fig. 10*. 1788. LECTOTYPE: *Q. regia* Vandelli ex Velloso = *Fuchsia regia* (Vandelli) Munz. Vandelli published the genus without naming a species. Munz (1943) designated *Fuchsia magellanica* as the lectotype, but that species occurs in Chile and Argentina, and Vandelli's publication was limited to Brazil. The illustration and description in Vandelli's book are in good agreement with *F. regia*.

Nahusia Schneevoogt, Icon. Pl. Rar. 1:21. 1792. TYPE: *N. coccinea* (Aiton) Schneevoogt = *Fuchsia coccinea* Aiton.

Thilcum Molina, Saggio Chili, ed. 2:146, 286. 1810. TYPE: *T. tinctorium* Molina = *Fuchsia magellanica* Lamarck.

Brebissonia Spach, Hist. Nat. Vég. Phan. 4:401. 1835, nom. rejic. TYPE: *B. microphylla* (Humboldt, Bonpland & Kunth) Spach = *Fuchsia microphylla* Humboldt, Bonpland & Kunth.

Kierschlegeria Spach, Hist. Nat. Vég. Phan. 4:403. 1835. TYPE: *K. lycioides* (Andrews) Spach = *Fuchsia lycioides* Andrews.
Lyciopsis Spach, Ann. Sci. Nat. Bot., sér. 2. 4:176. 1835. TYPE: *L. thymifolia* (Humboldt, Bonpland & Kunth) Spach = *Fuchsia thymifolia* Humboldt, Bonpland & Kunth.
Schufia Spach, Hist. Nat. Vég. Phan. 4:411. 1835. TYPE: *S. arborescens* (Sims) Spach = *Fuchsia arborescens* Sims.
Encliandra Zuccarini, Abh. Math. Phys. Cl. Königl. Bayer. Akad. Wiss. 2:335. 1837. TYPE: *E. parviflora* Zuccarini = *Fuchsia encliandra* Steudel.
Kirschlegeria H. G. L. Reichenbach, Handb. 246. 1837, orth. var. = *Kierschlegeria* Spach.
Myrinia Lilja, Fl. Sver. Suppl. 1:25. 1840, nom. rejic. TYPE: *M. microphylla* (Humboldt, Bonpland & Kunth) Lilja = *Fuchsia microphylla* Humboldt, Bonpland & Kunth.
Spachia Lilja, Tidning Trädgådsskötsel allmän Wextkultur 8:62. 1840, nom. illeg., non *Spachea* Jussieu. 1838. TYPE: *S. fulgens* (DeCandolle) Lilja = *Fuchsia fulgens* DeCandolle.
Ellobium Lilja, Linnaea 15:262. 1841, non *Ellobum* Blume. 1826, nom. rejic. Based on *Spachia* Lilja. 1840.
Quilusa J. D. Hooker, J. Linn. Soc., Bot. 10:460. 1869, orth. var. = *Quelusia* Vandelli 1788.

Erect to scandent shrubs, epiphytes, small- to medium-sized trees or procumbent creepers. Stems swollen or with tuberous underground parts in some species. Leaves simple, alternate, opposite, or whorled, with small, generally deciduous stipules. Flowers hermaphroditic, gynodioecious, or dioecious; actinomorphic, pedicellate, axillary or in racemose, paniculate, or involucrate inflorescences. Floral tube cylindric to obconic, deciduous in fruit. Sepals 4, valvate. Petals 4 or 0, convolute or spreading at anthesis. Stamens 8, biseriate, the antesepalous ones usually longer than the antepetalous ones, all erect or the antepetalous ones reflexed and included in the floral tube. Anthers oblong to reniform, bilocular, dorsifixed, longitudinally and introrsely dehiscent. Pollen shed singly, 2–4 porate, with beaded to smooth viscin threads. Nectary present at the base of the floral tube. Ovary 4-locular, ovules ca. 8–400, (uni-) bi- to multiseriate. Stigma usually exserted, capitate, globose, or clavate, 4-lobed or subentire. Fruit a berry; seeds 6–ca. 400 per fruit, triangular to compressed in cross-section, obovoid to ellipsoid or irregularly triangular in outline. Basic chromosome number $x = 11$; gametic chromosome numbers $n = 11$, 22, and 44.

Distribution (Figs. 1 and 2): Mostly cool, montane habitats in the Andes from Tierra del Fuego (55°S) to northern Colombia and Venezuela; in Central America and Mexico from central Panama to just north of the Tropic of Cancer (23°30′N); the coastal mountains of SE Brazil. Two species in Hispaniola, one species in central, coastal Chile; three species in New Zealand; one species in Tahiti. In the southern tip of South America and in coastal Chile, species descend to sea level.

The genus consists of nine sections, as outlined with their respective numbers and geographical ranges in Table 2. The following systematic treatment covers the main Andean section, sect. *Fuchsia*.

Fuchsia sect. **Fuchsia**

Fuchsia sect. *Quelusia* (Vandelli) DeCandolle, sensu DeCandolle, Prodr. 3:36. 1828, pro parte.
Fuchsia b. *Fuchsia* Zuccarini ex Endlicher, Gen. Pl. 1193. 1840.
Fuchsia sect. *Fuchsia* Zuccarini ex Walpers, Repert. Bot. Syst. 2:94, 1843.
Fuchsia sect. *Eufuchsia* Baillon, Hist. Pl. 6:467. 1877. Munz, Proc. Calif. Acad. Sci. IV. 25:15. 1943, pro parte.
Fuchsia sect. *Fuchsia*; Munz, N. Am. Flora II. 5:4. 1965, pro parte.

Erect, scandent, or climbing shrubs, subshrubs, or small trees. Leaves op-

posite or whorled. Flowers hermaphroditic, brightly (usually reddish) colored, divergent to pendant, axillary or arranged in racemose, paniculate, or involucrate inflorescences. Floral tubes longer than the sepals (except in *F. verrucosa*). Petals present and well developed, usually more than one-half as long as the sepals. Stamens erect, shorter than the sepals or slightly exserted beyond them. Nectary annular and mostly free from the floral tube, unlobed or shallowly 4–8-lobed, rarely an uneven band lining the base of the tube (in *F. magdalenae*) or composed of 4 or 8 prominent lobes adnate to the floral tube (in *F. pringsheimii* and *F. verrucosa*). Berry with ca. 50–250 seeds, the seeds compressed laterally and irregularly triangular-oblong in outline. Gametic chromosome numbers $n = 11, 22$.

Distribution (Figs. 1 and 2): Cloud forest of the tropical Andes from northern Argentina to Colombia and Venezuela; Hispaniola.

Unless otherwise indicated, measurements used in the key and species descriptions are based on dried herbarium specimens. In some characters such as floral tube thickness, stipule dimensions, and petal dimensions, this may represent a substantial reduction in size compared to living material, so certain compensation must be allowed when using living specimens. The key is almost entirely based on floral and foliar characters; since flowering and vegetative growth in sect. *Fuchsia* are essentially aseasonal, specimens are almost always collected with both leaves and flowers, so that lack of plant parts used in the key is rarely a problem. Floral tube length is measured from the top of the ovary to the rim of the tube, where the stamens and petals are inserted. Measurements of the antesepalous staminal filaments always precede those of the (shorter) antepetalous ones, and the number of secondary leaf veins always refers to the number of *each* side of the midvein.

The lack of major morphological differences and the overall similarity and variability in many species of sect. *Fuchsia* makes their separation by a simple key problematical, but a wide variety of characters are used when it is thought that the use of just one or two characters may be misleading. A number of dichotomies in the key are bridged by the variation present in certain species; in these cases, the species are keyed out under both entries.

Literature citations in the synonymy of each species are limited to the major floristic or revisionary treatments of the genus and to those references in which illustrations of the species are provided.

Since this paper covers a large number of taxa, some of them still poorly known, I have chosen not to recognize any taxa of subspecific rank. All the subspecific categories used by Munz (1943) were found to lie within the normal and continuous variation of their respective species. As with the other recent treatments in the family Onagraceae, considerably greater systematic knowledge of each species is required before subspecies are considered to be taxonomically meaningful units.

KEY TO THE SPECIES OF *FUCHSIA* SECT. *FUCHSIA*

1a. Flowers axillary and subtended by normal or slightly reduced leaves, *not* tightly clustered at the branch tips, on short, lateral branches, or in definite inflorescences. ---------- 2

1b. Flowers tightly clustered at the branch tips, in definite racemes, panicles, involucres, or on short, lateral, raceme-like branches. ---------- 41

2a. Floral tube 3–32 mm long. ---- 3
2b. Floral tube 33–80 mm long. ---- 13
3a. Floral tube 3–6 mm long, shorter than the ovary. ---- (61) *F. verrucosa*
3b. Floral tube 10–32 mm long, longer than the ovary. ---- 4
4a. Floral tube obconic, 9–16 mm wide at the rim; sepals 18–25 mm long; Hispaniola. ---- (60) *F. pringsheimii*
4b. Floral tube cylindric to narrowly funnelform, 2–9 mm wide at the rim; sepals 6–17 mm long; South America. ---- 5
5a. Branching well-developed and strongly divaricate, with short tertiary branchlets; leaves 15–35(–45) mm long, 7–15 mm wide; secondary veins 4–6 on either side of the midvein; central to southern Peru. ---- (1) *F. decussata*
5b. Branching more or less lax and not strongly divaricate, short tertiary branchlets usually lacking; leaves generally more than 40 mm long, more than 15 mm wide; secondary veins 6–15 on either side of the midvein. ---- 6
6a. Leaves opposite, very rarely ternate, the blade conspicuously rugulose; stems, leaves, and flowers with stiff, white, hispid pubescence; flowers 2–6 per branch. ---- (6) *F. scabriuscula*
6b. Leaves not entirely opposite, whorls of 3 or 4 usually present. The blades not conspicuously rugulose; pubescence not hispid, or lacking; flowers generally 8 or more per branch. ---- 7
7a. Young stems and leaves glabrous or occasionally lightly pubescent, the leaves sometimes villous on the adaxial midrib. ---- 8
7b. Young stems and leaves canescent, strigose, or ferrugineous-pilose. ---- 9
8a. Leaves firmly membranous, elliptic to oblanceolate, the margin entirely or obscurely denticulate; petiole 5–25 mm long; flowers uniformly bright orange or scarlet; Peru and Bolivia. ---- (4) *F. sanctae-rosae*
8b. Leaves thinly membranous, elliptic-ovate, the margin gland-denticulate; petiole (15–)25–50 mm long; tube and sepals pale whitish-pink, the petals darker red to purple; Colombia and Ecuador. ---- (10) *F. pallescens*
9a. Pedicels 3–10 mm long; ovary and berry narrowly cylindric-fusiform, the berry 13–25 mm long; young growth densely canescent. ---- 10
9b. Pedicels (6–)8–32 mm long; ovary ellipsoid, the berry ellipsoid to subglobose, 9–18 mm long; young growth not densely canescent. ---- 11
10a. Leaves mostly finely reticulate or rugulose; floral tube narrowly funnelform, 3.5–7 mm wide at the rim; sepals 10–13 mm long; petals red; berry tapered towards the apex, 13–17 mm long, 5–7 mm thick; Ecuador. ---- (9) *F. sylvatica*
10b. Leaves not rugulose, mostly sulcate-veined; floral tube subcylindric, 3–6 mm wide at the rim; sepals 6–10 mm long; petals deep purple; berry barely tapered at the apex, 15–25 mm long, 5–10 mm thick; Colombia and Venezuela. ---- (8) *F. nigricans*
11a. Leaf margin obscurely denticulate; stems canescent to finely pilose, hairs not reddish; ovary strongly tetragonous; petals oblong-elliptic to subrotund, (2–)3–8 mm wide; Ecuador. ---- (5) *F. loxensis*
11b. Leaf margin distinctly denticulate or serrulate; stems mostly strigose-pilose, with white to reddish hairs; ovary terete or slightly angled; petals lanceolate to elliptic, 2–3 mm wide; Peru. ---- 12
12a. Basal leaves mostly quaternate and considerably larger than the upper ones, not bluish-tinged; secondary veins 8–14 on either side of the midvein; flowers grouped towards the branch tips and subtended by somewhat reduced leaves; flowers pink to red, the floral tube 4–6 mm wide at the rim; Dept. Amazonas (Peru). ---- (3) *F. fontinalis*
12b. Basal leaves mostly ternate and not much larger than the upper leaves, often bluish-tinged; secondary veins 6–10 on either side of the midvein; flowers subtended by normal leaves and not grouped at the branch tips; flowers red to blue violet, the floral tube usually 6–9 mm wide at the rim; Depts. San Martín to Junín (Peru). ---- (2) *F. ferreyrae*
13a. Leaves sessile or subsessile, the petioles 0.5–3 mm long. ---- 14
13b. Leaves not sessile or subsessile, the petioles more than 3 mm long. ---- 16
14a. Leaves 10–50 mm wide, the margin denticulate or serrulate, not revolute; stems glabrous to puberulent; Bolivia. ---- (37) *F. cochabambana*
14b. Leaves 2–6 mm wide, the margin subentire or revolute; stems ferrugineous-pilose; Ecuador and Peru. ---- 15

15a. Leaves elliptic-ovate, 8–12 mm long, 3–5 mm wide; pedicels 9–15 mm long; northern Peru. ---------- (33) *F. confertifolia*
15b. Leaves linear, 20–70 mm long, 2–3 mm wide; pedicels 16–20 mm long; southern Ecuador. ---------- (7) *F. steyermarkii*
16a. Petals broad, less than twice as long as wide, the apex rounded to broadly acute. ---------- 17
16b. Petals narrow, more than twice as long as broad, the apex narrowly to broadly acute. ---------- 28
17a. Sepals strongly reflexed soon after anthesis; petals erect; central Ecuador. ---------- (27) *F. ampliata*
17b. Sepals suberect to divergent, not strongly reflexed after anthesis; petals spreading to divergent. ---------- 18
18a. Leaves entirely opposite, generally (narrowly) ovate; southern Peru. ---------- (48) *F. vargasiana*
18b. Leaves not entirely opposite, whorls of 3 or 4 usually present, mostly not ovate. ---- 19
19a. Secondary leaf veins mostly 3–8 on either side of the midvein. ---------- 20
19b. Secondary leaf veins mostly 8–22 on either side of the midvein. ---------- 24
20a. Petals usually longer than the sepals, rhombic to broadly elliptic, the base attenuate or unguiculate; leaves nitid on the upper surface, usually drying glossy and more or less bullate, margin markedly glandular-serrulate; southern Colombia to central Ecuador. ---------- (23) *F. corollata*
20b. Petals shorter or nearly equal to the sepals, not rhombic or with an attenuate or unguiculate base; leaves generally not drying glossy and bullate on the upper surface. ---------- 21
21a. Petals elliptic-ovate, usually markedly shorter than the sepals, 5–6(–9) mm wide; ovary terete or subterete, 5–6 mm long; leaf margin generally conspicuously gland-serrulate; floral tube pink cerise to purple lavender, often more or less strongly dilated near the middle; petals usually considerably darker than the sepals; southern Colombia. ---------- (24) *F. caucana*
21b. Petals orbicular to broadly elliptic-(ob-)ovate, only slightly shorter than the sepals, (6–)7–13 mm wide; ovary strongly tetragonous, 6–9 mm long; leaf margin subentire to gland-serrulate; floral tube orange to deep red, usually not strongly dilated near the middle; petals about the same color as the sepals. ---------- 22
22a. Leaves opposite or ternate, the margin gland-serrulate; pedicels 10–15 mm long; southern Ecuador. ---------- (36) *F. harlingii*
22b. Leaves 3–5-verticillate, margin subentire to denticulate; pedicels 5–55 mm long. ---- 23
23a. Pedicels mostly somewhat tuberculate, 14–55 mm long; floral tube somewhat verrucose, 4–6 mm wide at the base, 10–12 mm wide at the rim, densely villous inside in the lower ¼–½; sepals thick-spongy, ca. 1.5 mm thick when fresh; petals usually drying purplish; berry 16–18 mm long, 8–11 mm thick; southern Peru to Bolivia. ---------- (35) *F. austromontana*
23b. Pedicels smooth, 5–25(–40)mm long; floral tube smooth, 3–4 mm wide at the base, 6–10 mm wide at the rim, pilose inside for most of the length; sepals membranous, less than 1 mm thick when fresh; petals not drying purplish; berry 11–15 mm long, 7–9 mm thick; southern Colombia and Ecuador. ---------- (26) *F. vulcanica*
24a. Floral tube 5–8 cm long, usually somewhat recurved; sepals 7–8 mm wide at the base; leaves mostly opposite, 6–27 cm long; Ecuador and Colombia. ---------- (38) *F. macrostigma*
24b. Floral tube 3.5–6 cm long, straight; sepals 3.5–7 mm wide at the base; leaves mostly in whorls of 3 or 4, 2–18 cm long. ---------- 25
25a. Young stems and leaves glabrous or very lightly strigose; nectary non-annular, a smooth band 3–6 mm high lining the base of the tube; northeastern Colombia. ---------- (39) *F. magdalenae*
25b. Young stems and leaves markedly pubescent; nectary annular, 1–3 mm high and mostly free from the base of the tube; southern Colombia to Bolivia. ---------- 26
26a. Petals 8–11 mm long, 5.5–8 mm wide, considerably smaller than the sepals; floral tube 5–8 mm wide at the rim; stems and leaves canescent-strigose to hirtellous with mostly appressed hairs; leaves 6–18 cm long, 2.2–7 cm wide. ---------- (25) *F. ayavacensis*
26b. Petals 12–17 mm long, 8–13 mm wide, nearly as long as the sepals; floral tube 8–12 mm wide at the rim; stems and leaves subglabrous to densely pubescent, the hairs usually more or less erect; leaves 2.5–8(–10) cm long, 1–4 cm wide. ---------- 27

27a. Leaves mostly glabrous on the upper surface; floral tube 4–6 mm wide at the base, somewhat tuberculate, the walls very firm and ca. 1.5 mm thick when fresh, the tube densely villous inside only in the lower ¼–⅓; petals usually drying purplish; berry 16–18 mm long when ripe; southern Peru to Bolivia. ---------- (35) *F. austromontana*

27b. Leaves pubescent on the upper surface; floral tube 3–4 mm wide at the base, smooth, the walls not very firm, less than 1 mm thick when fresh, the tube pilose inside for most of its length; petals not drying purplish; berry 11–15 mm long; Ecuador. ---------- (26) *F. vulcanica*

28a. Leaf margin entire or more or less revolute, glandular teeth not visible without a lens. ---------- 29

28b. Leaf margin denticulate or serrate, glandular teeth clearly visible. ---------- 31

29a. Petals 9–11 mm long, smooth and not recurved; southern Ecuador. ---------- (32) *F. scherffiana*

29b. Petals 15–22 mm long, crispate-undulate and recurved when fresh. ---------- 30

30a. Secondary leaf veins 7–12 on either side of the midvein; leaves mostly ternate; sepal tips united in bud; Colombia and Venezuela. ---------- (28) *F. venusta*

30b. Secondary leaf veins 13–15 on either side of the midvein; leaves mostly quaternate; sepal tips mostly free and spreading in bud; northern Peru. ---------- (29) *F. rivularis*

31a. Leaves entirely opposite, generally (narrowly) ovate; northern Peru. ---------- (48) *F. vargasiana*

31b. Leaves not strictly opposite, whorls of 3 or 4 usually present, not ovate. ---------- 32

32a. Petals about as long or longer than the sepals. ---------- 33

32b. Petals distinctly shorter than the sepals. ---------- 38

33a. Petiole 3–9 mm long. ---------- 34

33b. Petiole 10–40 mm long. ---------- 36

34a. Secondary leaf veins 3–8 on either side of the midvein; Colombia and Ecuador ---------- (23) *F. corollata*

34b. Secondary leaf veins 9–15 on either side of the midvein; northern Peru. ---------- 35

35a. Leaves ternate or mostly quaternate; secondary veins 13–15 on either side of the midvein; margin entire to denticulate; stems smooth. ---------- (29) *F. rivularis*

35b. Leaves opposite or ternate; secondary veins 9–13 on either side of the midvein; margin dentate; stems verrucose. ---------- (31) *F. llewelynii*

36a. Floral tube slightly striated-tuberculate, hirtellous, 3.5–5.5 mm wide at the base, 1–2 mm thick and firm-spongy when fresh, dull orange; pedicels 5–13 mm long; southern Colombia. ---------- (57) *F. canescens*

36b. Floral tube smooth, glabrous to strigose, 2.5–4 mm wide at the base, less than 1 mm thick and not firm-spongy when fresh, bright red to pink; pedicels 12–40 mm long. ---------- 37

37a. Petals elliptic to rhombic, (5–)6–10 mm wide; leaves firm, 2–7 cm long, 0.7–3 cm wide, usually drying more or less bullate and glossy on the upper surface; petioles 3–12(–22) mm long; southwestern Colombia and Ecuador. ---------- (23) *F. corollata*

37b. Petals elliptic-lanceolate to slightly obovate, 4–8 mm wide; leaves thin, 3.5–12 cm long, 1.5–5 cm wide, dull and not bullate when dry; petioles 10–48 mm long; Venezuela and northeastern Colombia. ---------- (30) *F. gehrigeri*

38a. Floral tube subcylindric, (3–)4–8 mm wide at the base, the walls very firm and 1–1.5 mm thick when fresh; ovary 10–13 mm long; anthers 4–6 mm long; Peru and Bolivia. ---------- (34) *F. denticulata*

38b. Floral tube funnelform 2–4(–6) mm wide at the base, the walls not very firm, less than 1 mm thick when fresh; ovary 5–8 mm long; anthers 2–4 mm long; Colombia and Ecuador. ---------- 39

39a. Young branches angled, densely cinereous-pubescent; leaves mostly quaternate; floral tubes 5–6(–8) mm wide at the rim; sepals 3–4 mm wide at the base; Colombia-Ecuador border area. ---------- (58) *F. cinerea*

39b. Young branches terete, not densely cinereous; leaves mostly ternate; floral tubes (4–)6–12 mm wide at the rim; sepals 5–9 mm wide at the base. ---------- 40

40a. Petals elliptic-ovate, 9–11(–14) mm long, obtuse to cuneate at the apex, glabrous, purplish and usually darker than the sepals; sepals 5–6 mm wide at the base; southern Colombia. ---------- (24) *F. caucana*

40b. Petals lanceolate to lance-elliptic, (8–)12–20 mm long, mostly acute at the apex, usually finely puberulent or villous on the dorsal surface, red and not much darker than the sepals; sepals mostly 6–9 mm wide at the base; central Colombia and Venezuela. ---------- (22) *F. petiolaris*

41a. Floral tubes 12–23 mm long. ---------- 42

41b. Floral tubes 24–130 mm long. ---------- 58

42a. Leaves sessile or subsessile, the petiole 0.5–5 mm long; secondary veins 18–25 on either side of the midvein. ---- (44) *F. sessilifolia*
42b. Leaves not sessile or subsessile, the petiole more than 5 mm long; secondary veins 5–18 on either side of the midvein. ---- 43
43a. Leaves entirely or mostly opposite. ---- 44
43b. Leaves mostly 3–4-verticillate. ---- 49
44a. Secondary leaf veins 3–8 on either side of the midvein; floral tube pale cream to pink, the petals much darker than the sepals. Ecuador and southern Colombia. ---- (10) *F. pallescens*
44b. Secondary leaf veins 9 or more on either side of the midvein; floral tube red to orange, not pale or whitish, the petals not much darker than the tube and sepals. ---- 45
45a. Stems and leaves densely pilose; leaves mostly ovate. ---- 46
45b. Stems and leaves not densely pilose, subglabrous to puberulent or strigillose; leaves mostly elliptic, not ovate. ---- 47
46a. Flowers in a compact, terminal raceme 1.5–7 cm long; pedicels 18–30 mm long; sepals 7–9 mm long; southern Peru. ---- (46) *F. tincta*
46b. Flowers in axillary racemes or panicles 5–10 cm long; pedicels 10–20 mm long; sepals 10–13 mm long; Central Peru. ---- (15) *F. ovalis*
47a. Flowers in axillary racemes or on short side branches, the subtending leaves not strongly reduced or modified; Peru. ---- (13) *F. macrophylla*
47b. Flowers in terminal racemes with strongly reduced, subsessile, linear to lanceolate bracts; Colombia and Ecuador. ---- 48
48a. Racemes generally elongate, 5–16 cm long, the bracts persistent; pedicels 3–7(–12) mm long, usually not divergent; sepals 6–8 mm long; secondary leaf veins 12–17 on either side of the midvein. ---- (11) *F. orientalis*
48b. Racemes generally compact, 1–4(–10) cm long, the bracts mostly deciduous; pedicels divergent, 8–25 mm long; sepals 8–11 mm long; secondary leaf veins 9–13 on either side of the midvein. ---- (17) *F. putumayensis*
49a. Pedicels 2–10 mm long. ---- 50
49b. Pedicels 10–40 mm long. ---- 54
50a. Leaves mostly in whorls of 4; flowers generally paniculate or densely crowded on the ultimate branches; berries subglobose, 6–10 mm long. ---- 51
50b. Leaves mostly in whorls of 3; flowers racemose, few racemes on each plant; berries oblong to cylindrical, 13–25 mm long. ---- 52
51a. Leaves 4 or more per whorl, the margin slightly denticulate; stems canescent to hirtellous; floral tube 13–20(–24) mm long, 1.5–3 mm wide at the base; Colombia. ---- (55) *F. hartwegii*
51b. Leaves 4 or less per whorl, the margin markedly denticulate to serrate; stems canescent to densely pilose; floral tube 15–28 mm long, 3–4 mm wide at the base; northern Peru. ---- (3) *F. fontinalis*
52a. Stems, leaves, and flowers densely pilose-hirsute; ovary 5–6 mm long; bracts narrowly lanceolate; northern Peru. ---- (16) *F. pilosa*
52b. Stems, leaves, and flowers usually canescent or strigillose, never pilose or hirsute; ovary (6–)7–11 mm long; bracts ovate to elliptic; Venezuela to Ecuador. ---- 53
53a. Leaves usually finely reticulate or rugulose; floral tube narrowly funnelform, 3.5–7 mm wide at the rim; sepals 10–13 mm long; petals red; berries tapered towards the apex, 13–17 mm long, 5–7 mm thick; Ecuador. ---- (9) *F. sylvatica*
53b. Leaves not finely reticulate or rugulose; floral tube subcylindric, 3–6 mm wide at the rim; sepals 6–10 mm long; petals dark purple; berries barely tapered at the apex, 15–25 mm long, 5–10 mm thick; Colombia and Venezuela. ---- (8) *F. nigricans*
54a. Leaves and branchlets glabrous or finely puberulent, except for hairs sometimes on the adaxial leaf midvein. ---- 55
54b. Leaves and branchlets canescent to hirtellous or densely pilose. ---- 56
55a. Flowers red, in axillary racemes or on short, lateral branches; leaves 5–9 cm wide; secondary veins 14–19 on either side of the midvein; central Peru. ---- (13) *F. macrophylla*
55b. Flowers orange red, generally axillary, not in axillary racemes or on short side branches; leaves 1–4 cm wide, secondary veins 6–15 on either side of the midvein; southern Peru to Bolivia. ---- (4) *F. sanctae-rosae*
56a. Leaves broadly elliptic to ovate; flowers in axillary racemes or panicles; central Peru. ---- (15) *F. ovalis*
56b. Leaves lanceolate to elliptic, not ovate; flowers in terminal racemes or panicles. ---- 57

57a. Leaves 4 or more per whorl, the margin slightly denticulate; stems canescent to hirtellous; floral tube 13–20(–24) mm long, 1.5–3 mm wide at the base; Colombia. ---- (55) *F. hartwegii*
57b. Leaves 4 or less per whorl, the margin markedly denticulate to serrate; stems canescent to densely pilose; floral tube 15–28 mm long, 3–4 mm wide at the base; northern Peru. ---------- (3) *F. fontinalis*
58a. Leaves sessile or subsessile, petioles 0.5–3 mm long. ---------- 59
58b. Leaves not sessile or subsessile, petioles more than 3 mm long. ---------- 62
59a. Leaves 8–12 mm long, 3–5 mm wide; stems pilose; northern Peru. ---- (33) *F. confertifolia*
59b. Leaves 30–120 mm long, 10–50 mm wide; stems glabrous or sparsely puberulent. ---------- 60
60a. Secondary leaf veins 4–5 on either side of the midvein; central Peru. ---------- (42) *F. coriacifolia*
60b. Secondary leaf veins 8–26 on either side of the midvein. ---------- 61
61a. Leaves 10–24 cm long, 4–8 cm wide, the margin entire; Ecuador and northern Peru. ---------- (12) *F. glaberrima*
61b. Leaves 3–6 cm long, 1–5 cm wide, the margin denticulate or serrate; Bolivia. ---------- (37) *F. cochabambana*
62a. Leaves entirely or mostly opposite. ---------- 63
62b. Leaves mostly in whorls of 3 or more. ---------- 81
63a. Floral tube 9–13 cm long; flowers in involucres with concave, sessile bracts; central Peru. ---------- (41) *F. ceracea*
63b. Floral tube less than 9 cm long; flowers not involucrate with sessile, concave bracts. ---- 64
64a. Flowers in axillary racemes or on short, lateral branches. ---------- 65
64b. Flowers in terminal racemes or panicles, not in axillary racemes or short, lateral branches. ---------- 66
65a. Floral tube 19–25 mm long; sepals 8–9 mm long, green-tipped; berry subglobose, 10–13 mm long, 8–9 mm thick. ---------- (13) *F. macrophylla*
65b. Floral tube 32–45 mm long; sepals 10–13 mm long, red; berry ellipsoid, 15–17 mm long, 7–10 mm thick. ---------- (14) *F. macropetala*
66a. Rachis elongate, 10–60 cm long. ---------- 67
66b. Rachis compact, 0.5–10 cm long. ---------- 70
67a. Secondary leaf veins 15–22 on either side of the midvein. ---------- 68
67b. Secondary leaf veins 8–14 on either side of the midvein. ---------- 69
68a. Petioles 4–10 mm long; sepals divergent after anthesis. ---------- (21) *F. abrupta*
68b. Petioles 20–70 mm long; sepals strongly reflexed after anthesis. ---- (49) *F. boliviana*
69a. Leaves generally strigillose, 2.5–10(–13) cm long, 1–5 cm wide; floral tubes generally dilated near the middle and slightly constricted at the rim; petals 6–9 mm long; Hispaniola. ---------- (59) *F. triphylla*
69b. Leaves soft pilose, 7–18 cm long, 2–8 cm wide; floral tubes narrowly funnelform, not strongly dilated near the middle or constricted at the apex; petals 11–20 mm long; northern Peru. ---------- (51) *F. wurdackii*
70a. Secondary leaf veins mostly 3–7 on either side of the midvein; floral tube and sepals pale pink, petals purple. ---------- (10) *F. pallescens*
70b. Secondary leaf veins mostly 7–22 on either side of the midvein; floral tube and sepals not pale pink, petals not purple. ---------- 71
71a. Stems and leaves glabrous, puberulent, or velutinous. ---------- 72
71b. Stems and leaves coarsely pubescent (pilose, tomentose, or hispidulous). ---------- 79
72a. Floral tube 40–70 mm long. ---------- 73
72b. Floral tube 32–40 mm long. ---------- 74
73a. Leaves glossy, glabrous on the upper surface; secondary veins 8–12 on either side of the midvein; stems subglabrous; Colombia. ---------- (20) *F. cuatrecasasii*
73b. Leaves not glossy, usually strigillose or velutinous on the upper surface; secondary veins 13–17 on either side of the midvein; stems generally puberulent; central Peru. ---------- (50) *F. corymbiflora*
74a. Racemes (4–)5–15 cm long, suberect to nodding; leaves strigillose to subpilose; Hispaniola. ---------- (59) *F. triphylla*
74b. Racemes 2–5(–10) cm long, divergent to pendant, not suberect; leaves glabrous to puberulent; South America. ---------- 75
75a. Leaves oblanceolate, 10–24 cm long, 4–8 cm wide, often purple-flushed below; petioles stout, 3–8 mm long; ovary 7–9 mm long; stipules thick, persistent; Ecuador and northern Peru. ---------- (12) *F. glaberrima*
75b. Leaves mostly elliptic, 4–17 cm long, 2–10 cm wide, usually not purple-flushed below;

petioles not stout, 4–30 mm long; ovary 2.5–7 mm long; stipules not thick and persistent. ---- 76

76a. Petals 4–6 mm wide; ovary 4–7 mm long; floral tube (28–)35–40 mm long; southern Colombia. ---- (20) *F. cuatrecasasii*

76b. Petals 2.5–4 mm wide; ovary 2.5–4 mm long; floral tube 23–35(–40) mm long; northern Peru to southern Colombia. ---- 77

77a. Leaves elliptic to obovate, 2–10 cm wide, mostly opposite; sepals lanceolate, 3–5 mm wide. ---- 78

77b. Leaves narrowly elliptic to narrowly (ob-)lanceolate, 1–4 cm wide, whorls of 3 or 4 usually present; sepals narrowly lanceolate, 2.5–4 mm wide; southern Ecuador. -- (18) *F. lehmannii*

78a. Branchlets finely puberulent; secondary leaf veins 9–13 on either side of the midvein; petioles 6–15 mm long; floral tube 15–27 mm long; southern Colombia to central Ecuador. ---- (17) *F. putumayensis*

78b. Branchlets mostly strigillose; secondary leaf veins (8–)12–15 on either side of the midvein; petioles 6–30 mm long; floral tube 23–40 mm long; southern Ecuador and northern Peru. ---- (19) *F. andrei*

79a. Ovary narrowly cylindric, 10–11 mm long; berry narrowly cylindric-fusiform, often more or less curved or with a strongly narrowed apex, 25–32 mm long; secondary leaf veins 12–18 on either side of the midvein; southern Peru. ---- (48) *F. vargasiana*

79b. Ovary oblong, 5–10 mm long; berry oblong to globose, 12–20 mm long, not curved or with a strongly narrowed apex; secondary leaf veins 7–14 on either side of the midvein. ---- 80

80a. Rachis 4–18 cm long; pedicels 9–11(–25) mm long; petals 9–16 mm long; leaf margin subdenticulate; stipules conspicuous, 3–5 mm long; northern Peru. ---- (51) *F. wurdackii*

80b. Rachis 1.5–5 cm long; pedicels 15–40 mm long; petals 6–10 mm long; leaf margin denticulate or serrulate; stipules 2–3 mm long; Bolivia. ---- (47) *F. furfuracea*

81a. Flowers in involucres with sessile, concave bracts. ---- 82

81b. Flowers not in involucres with sessile, concave bracts. ---- 83

82a. Floral tube 4–5 cm long; petals 9–13 mm long. ---- (40) *F. simplicicaulis*

82b. Floral tube 9–13 cm long; petals 5–7 mm long. ---- (41) *F. ceracea*

83a. Floral tubes 23–30 mm long. ---- 84

83b. Floral tubes 30–76 mm long. ---- 87

84a. Petioles (15–)25–50 mm long, secondary leaf veins 5–7(–9) on either side of the midvein; tube and sepals pale pink-cream, the petals much darker and purple. ---- (10) *F. pallescens*

84b. Petioles 4–20(–25) mm long; secondary leaf veins 7–14 on either side of the midvein; tube and sepals not pale pink-cream, the petals not purple or much darker than the sepals. ---- 85

85a. Young stems and leaves mostly pilose; leaf margin conspicuously gland-denticulate or serrulate; floral tube widest at the rim, where 4–6 mm wide; northern Peru. ---- (3) *F. fontinalis*

85b. Young stems and leaves glabrous to strigose; leaf margin entire to finely denticulate; floral tube usually widest below the rim, 6–11 mm wide at the rim. ---- 86

86a. Flowers densely crowded on short, divergent to pendant racemes 0.5–3 cm long; petals narrowly lance-oblong, 2.5–4 mm wide; southern Ecuador. -- (18) *F. lehmannii*

86b. Flowers generally not densely crowded, racemes suberect to nodding and 4–15 cm long; petals elliptic-ovate, 4–6 mm wide; Hispaniola. ---- (59) *F. triphylla*

87a. Leaves entirely or mostly in whorls of 4 or more. ---- 88

87b. Leaves entirely or mostly in whorls of 3. ---- 93

88a. Petioles 12–35 mm long. ---- 89

88b. Petioles 3–10(–15) mm long. ---- 91

89a. Sepals 14–18 mm long, 6–9 mm wide at the base, thick-spongy and somewhat verrucose when fresh; petals trowel-shaped, 14–19 mm long, 4–7 mm wide; southern Colombia. ---- (57) *F. canescens*

89b. Sepals 11–14 mm long, 3–6 mm wide at the base, not thick-spongy or verrucose when fresh; petals narrowly lanceolate to narrowly elliptic-oblong, 11–16(–18) mm long, 3–5(–6) mm wide. ---- 90

90a. Young branches and leaves densely canescent to strigillose; leaves rarely more than 4 per whorl; stipules deciduous, not thick-callose when fresh, 1.5–2 mm long, 0.4–0.5 mm wide; southern Colombia and Ecuador. ---- (53) *F. dependens*

90b. Young branches and leaves sparsely strigillose to strigose; leaves often more than 4 leaves per whorl; stipules thick-callose when fresh, persistent and recurved at the older nodes, 2.5–4 mm long, ca. 3 mm wide; central Colombia. ---------- (56) *F. crassistipula*

91a. Flowers subracemose, not in panicles; pedicels 10–53 mm long; northern Peru. ---------- (29) *F. rivularis*

91b. Flowers in panicles; pedicels 4–12 mm long. ---------- 92

92a. Young stems and leaves hirtellous to strigillose; central Colombia. -- (54) *F. hirtella*

92b. Young stems and leaves finely puberulent to subglabrous; Ecuador and southernmost Colombia. ---------- (45) *F. polyantha*

93a. Secondary leaf veins 15–25 on either side of the midvein. ---------- 94

93b. Secondary leaf veins 7–15 on either side of the midvein. ---------- 95

94a. Petioles 4–10 mm long; sepals not reflexed after anthesis; pedicels divergent to ascending. ---------- (21) *F. abrupta*

94b. Petioles 20–70 mm long; sepals strongly reflexed after anthesis; pedicels pendant. ---------- (49) *F. boliviana*

95a. Petals distinctly shorter than the sepals. ---------- 96

95b. Petals nearly as long or longer than the sepals. ---------- 98

96a. Floral tube 55–76 mm long; central Peru. ---------- (43) *F. sanmartina*

96b. Floral tube 22–40 mm long. ---------- 97

97a. Flowers tightly grouped in a raceme 0.5–3 cm long; petals 2.5–4 mm wide; southern Ecuador. ---------- (18) *F. lehmannii*

97b. Flowers not tightly grouped, racemes 4–15 cm long; petals 4–6 mm wide; Hispaniola. ---------- (59) *F. triphylla*

98a. Petioles 10–48 mm long. ---------- 99

98b. Petioles mostly 2–10 mm long. ---------- 100

99a. Pedicels generally short, 9–11(–25) mm long; ovary cylindrical, 7–10 mm long; leaves soft pilose, 7–18 cm long; stipules pale, 3–5 mm long and persistent; northern Peru. ---------- (51) *F. wurdackii*

99b. Pedicels 12–40 mm long; ovary ovoid, often constricted near the apex, 5–7 mm long; leaves membranous, subglabrous to strigillose, 3.5–12 cm long; stipules dark, 1.5–2 mm long, often deciduous; Venezuela. ---------- (30) *F. gehrigeri*

100a. Leaves mostly in whorls of 4, secondary veins 13–15 on either side of the margin; sepal tips usually free and spreading in bud; anthers narrowly oblong, 4–4.5 mm long; northern Peru. ---------- (29) *F. rivularis*

100b. Leaves mostly in whorls of 3; secondary veins 7–12 on either side of the midvein; sepal tips usually connate in bud; anthers oblong, 2–3.5 mm long. ---------- 101

101a. Young stems and leaves densely pilose, often with reddish hairs; leaves narrowly elliptic to oblanceolate, often somewhat curved to one side; not glossy; northern Peru. ---------- (52) *F. mathewsii*

101b. Young stems and leaves subglabrous to finely hirtellous, never with reddish hairs; leaves elliptic, symmetrical, glossy on both sides; Colombia and Venezuela. ------- (28) *F. venusta*

1. **Fuchsia decussata** Ruiz & Pavón, Fl. Peruv. Chil. 3:88, *pl. 323, fig. b.* 1802. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):552. 1941, pro parte. Munz, Proc. Calif. Acad. Sci. IV. 25:56, *pl. 8, fig. 44.* 1943, pro parte. TYPE: Peru, Dept. Huánuco, abundant at Muña, 1778–1788, *Hipólito Ruiz & José Pavón* (MA, lectotype, here designated; photograph, MO). There are five Ruiz and Pavón collections of this species at MA, four at BM, and one each at F, G, MO, and NY. Since there is no collection data on any of the sheets, it is not possible to determine which sheets may be duplicates, so no isolectotypes have been designated.

Fuchsia scandens K. Krause, Repert. Spec. Nov. Regni Veg. 1:171. 1905. TYPE: Peru, Dept. Huánuco, mountains SW of Monzón, 3,400–3,500 m, 1904–1920, *August Weberbauer 3324* (B, holotype, destroyed in World War II; photograph, F). The photograph shows a poor specimen with few leaves or flowers and branches covered with lichens. Though this entity might correspond to *F. ferreyrae*, its leaves are closer to those of *F. decussata,* which the description does not exclude.

Fuchsia fusca K. Krause, Bot. Jahrb. Syst. 37:599. 1906. TYPE: Peru, Dept. Cuzco, Prov. La Convención, below Yanamanche, near road from Cuzco to Santa Ana, 3,300–3,400 m, 1904–1920, *August Weberbauer 4975* (B, holotype, destroyed in World War II; photograph, F; G, isotype).

Suberect to scandent shrubs 1–3 m tall with a well-developed system of lateral, divaricate, often horizontal branches. Secondary and tertiary branches numerous, 2–4 per node and held at near 90° to stem, densely ferrugineous-tomentose to canescent; older stems 5–14 mm thick with sublustrous, copper red bark exfoliating in long, uneven strips. Leaves opposite or mostly ternate, firmly membranous, lanceolate to elliptic-obovate, acute to attenuate at the base, acute at the apex, 15–35(–45) mm long, 7–15 mm wide, usually dark green and subglabrous to strigillose above with impressed veins, paler below with strigose, usually reddish hairs along the veins; secondary veins 4–6 on either side of the midvein, subelevated below, higher order veins not visible without magnification, margin subentire to serrulate or denticulate. Petiole 3–10(–14) mm long, canescent to tomentose. Stipules filiform, 2–3 mm long, ca. 0.3 mm wide, mostly deciduous. Flowers axillary and few to numerous towards the tips of branches. Pedicels slender, strigose, at times slightly verrucose, arching-pendant, 15–25 mm long. Ovary oblong, 2–3 mm long, 1–1.5 mm thick. Floral tube subcylindric, 10–20(–23) mm long, 3–4 mm wide at the base, usually slightly narrowed to 2.5–3 mm wide above the nectary and slightly widened above to 4–6 mm wide at the rim, subglabrous to strigillose and occasionally verrucose outside, densely villous inside in lower ½–⅓. Sepals narrowly lanceolate, 8–10(–18) mm long, 2–3(–4) mm wide, narrowly acute at the apex, not much wider than the tube in bud, spreading at anthesis. Tube red to dark red, sepals red with dull green tips in bud. Petals scarlet to orange red, linear to broadly elliptic-ovate and often variable on the same plant, 5–9(–14) mm long, 1.5–4(–8) mm wide, apex acute. Nectary unlobed to obscurely 4-lobed, 1–1.5 mm high. Filaments red, 8–10 mm and 5–8 mm long; anthers oblong, 2–2.3 mm long, 1.2–1.5 mm wide, dull white. Style glabrous, red; stigma clavate to capitate, ca. 2 mm long and 1–2 mm wide, obscurely 4-cleft, white, exserted 4–8 mm beyond the anthers. Berry subglobose, subtetragonous before maturity, 8–9 mm long, 5–6 mm thick, red; seeds tan, 1.5–1.6 mm long, 0.8–1.0 mm wide.

Distribution: Peru. Scattered to locally frequent shrubs in thickets from tree line to mid-elevation cloud forest, from San Martín to Cuzco Depts., 2,900–3,400 m (Fig. 55).

Representative specimens examined: PERU, AYACUCHO: 19 km E of Tambo, *Berry 3049* (MO, USM); 40–46 km NNE of Tambo, *Luteyn & Lebrón-Luteyn 6352* (MO, NY); near Cusimachay, 25 km NE of Tambo, *Madison 10374-70* (MO); Sigsiqa, between Tambo and Ayna, *Tovar 6148* (USM). CUZCO: Km 157 of Cuzco-Quillabamba road, *Berry 2574* (CUZ, MO); Km 158 of Cuzco-Quillabamba road, *Berry & Aronson 3041* (MO, USM); between Yanamanche and Quellomayo, *Vargas 4512* (BH, CUZ, MO). HUÁNUCO: between Acomayo and Chinchao, *Ambrose et al. 2397* (BH); 3 km E of Carpish tunnel, *Berry & Aronson 3086* (MO, USM); Carpish, *Ferreyra 2093* (F, MO, NY, US, USM); Carpish, above Acomayo, *Hutchison & Wright 5944* (F, G, LE, MICH, MO, NY, P, RSA, UC, US, USM); Muña, *Pearce 513* (K); Tumanga, *Woytkowski 7984* (US). JUNÍN: 64 km above Satipo to Concepción, *Berry & Aronson 3075* (MO, USM). SAN MARTÍN: valley of Río Apisoncho, ca. 30 km above Jucusbamba, *Hamilton & Holligan 552* (K, S, UC), *1057* (K), *1093* (K, UC).

Fuchsia decussata is distinguished from other members of its species group

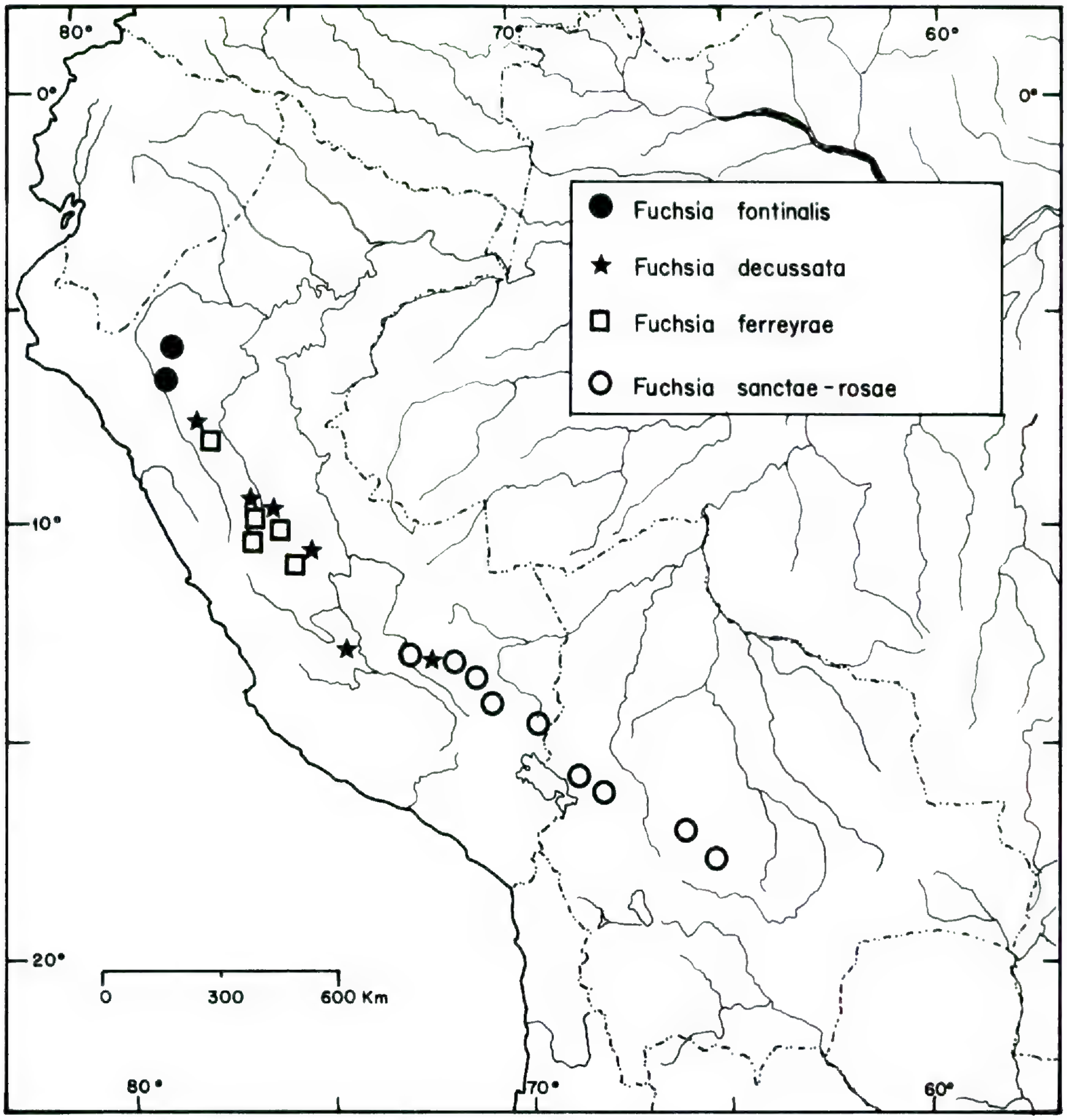


FIGURE 55. Distribution of the *Fuchsia decussata* species group.

by the small leaves with few secondary veins and the strongly divaricate branching pattern with short tertiary branchlets. It is closely allied to *F. ferreyrae*, and some intergradation between them may occur (see discussion under *F. ferreyrae*). It occurs sympatrically with *F. abrupta*, *F. corymbiflora*, *F. denticulata*, *F. ferreyrae*, and *F. sanmartina*.

Pubescence and petal size and shape vary considerably throughout the range of this species. Plants from the Carpish area in Huánuco have very narrow petals nearly as long as the sepals and a soft, reddish tomentum on the branches. Plants from Cuzco, such as the one described as *F. fusca*, have stiffer, more erect hairs, somewhat broader floral tubes, and wider petals. Extreme petal variation is found locally or in individual plants in Dept. Ayacucho. *Luteyn & Lebrón-Luteyn 6352* (MO, NY) has petals 14 mm long and 8 mm wide, while the petals of *Berry 3149*

(MO, USM) from the same area vary widely, at times approaching the narrowly lanceolate petals of the Huánuco populations.

Sandeman 4585 (K, OXF; Dept. Junín, above Huacapistana, ca. 2,000 m, Oct. 1943) is a possible hybrid with *F. abrupta*. The flowers are subracemose with narrowly cylindric ovaries as in *F. abrupta*, but the short tubes (ca. 25 mm long) and branching system indicate parentage of *F. decussata*. Both species are known from the area, and less than 5% of the pollen of the presumed hybrid is stainable. Another collection from the same locality, *Sandeman 4503* (K) is more similar to *F. abrupta*, except that it has short floral tubes less than 25 mm long.

2. **Fuchsia ferreyrae** P. Berry, **sp. nov.** TYPE: Peru, Dept. Junín, Prov. Satipo, 68 km W of Satipo on road to Concepción, 3,110 m, 2 Aug. 1978, *Paul Berry & James Aronson 3073* (MO 2720583, holotype; MO, USM, isotypes). Named after Dr. Ramón Ferreyra, Director of the Museo de Historia Natural "Javier Prado" in Lima, Peru, and long-time collector of the Peruvian flora. Fig. 27.

Fuchsia decussata sensu Munz, Proc. Calif. Acad. Sci. IV. 25:56. 1943, pro parte.

Frutex erectus vel scandens 1–3 m altus, ramis arcuato-patentibus 0.5–1.5 m longis. Ramuli subcanescentes vel dense strigosi pilis interdum rubris instructi. Folia 3–4-verticillata vel raro opposita, membranacea, reticulata, elliptica vel obovata, basi acuta vel acuminata apice acuta, 2–8 cm longa, 1–3 cm lata, superne atroviridia subtiliter strigulosaque, subtus nervis praesertim strigosis et pagina saepe cyanescenti; nervis secundariis utroque latere 6–10, margine obscure vel valde glanduloso-serrulata; petiolis 4–12 mm longis; stipulis filiformibus, 2–4 mm longis, deciduis. Flores atrorubri vel atroviolacei, axillares et numerosi ad apicem ramorum dispositi; pedicellis tenuibus dependentibusque, 12–30 mm longis. Tubi florales anguste infundibuliformes, (15–)22–28 mm longi, basi 3–4 mm lati et conspicue nodosi inde ca. 2 mm lati valde constricti, superne dilatati summo (6–)8–9 mm lati, extus strigulosi vel pilosi intus glabrati. Sepala anguste lanceolata, acuminata, (10–)14–16 mm longa, ca. 3 mm lata, alabastro saepe apicibus libris. Petala rubra vel violacea, elliptica, acuta, plerumque plus minusve dimidio breviora quam sepalis, 7–9 mm longa, ca. 3 mm lata. Filamenta antisepala 9–13 mm longa, antipetala 5–9 mm longa, antheris oblongis, ca. 2 mm longis ca. 1.5 mm latis. Stylus glaber, stigmate capitato, apice leviter 4-fisso, ca. 2 mm longo latoque, obscure albido. Bacca ellipsoidea vel subglobosa, ca. 12 mm longa, ca. 8 mm lata, nitens purpureaque; seminibus 1–1.2 mm longis, ca. 0.6 mm latis. Numerus gameticus chromosomatum $n = 11$.

Erect to climbing-scandent shrubs 1–3 m tall with horizontally divergent to arcuate branches 0.5–1.5 m long. Branchlets subcanescent to coarsely strigose with reddish hairs; older branches with finely fissured, dull tan to coppery bark. Leaves in whorls of 3 or 4, occasionally opposite or subopposite, membranous, elliptic to obovate, acute to attenuate at the base, acute at the apex, 2–8 cm long, 1–3 cm wide, velvety dark green and strigillose above, strigose below especially along veins and often flushed with a bluish tinge; secondary veins 6–10 on either side of the midvein, higher order veins reticulate and usually visible without magnification; margin moderately to strongly glandular-serrulate. Petiole pubescent, 4–12 mm long. Stipules filiform, 2–4 mm long, ca. 0.4 mm wide, deciduous. Flowers axillary and numerous towards the branch tips. Pedicels slender, pendant, 12–30 mm long. Ovary oblong, ca. 3 mm long. Floral tube narrowly funnelform, (15–)22–28 mm long, 3–4 mm wide and conspicuously nodose at the base, then ± abruptly narrowed to ca. 2 mm wide above the nectary and gradually widened above until (6–)8–9 mm wide at the rim, strigillose to pilose outside, glabrous inside. Sepals narrowly lanceolate, (10–)14–16 mm long, ca. 3 mm wide, acuminate, often with free tips in bud, divergent at anthesis. Tube and sepals dark red to deep violet (blue red). Petals red to violet, elliptic, usually about half

as long as the sepals, 7–9 mm long, ca. 3 mm wide, acute at the apex. Nectary unlobed, ca. 1.5 mm high. Filaments red to violet, 9–13 mm and 5–9 mm long; anthers oblong, ca. 2 mm long, ca. 1.5 mm wide. Style glabrous, red to violet; stigma capitate, ca. 2 mm long and wide, slightly 4-lobed, dull white. Berry ellipsoid to subglobose, ca. 12 mm long, ca. 8 mm thick, lustrous purple; seeds 1–1.2 mm long, ca. 0.6 mm wide. Gametic chromosome number $n = 11$.

Distribution: Central Peru. Locally frequent shrubs in openings of cloud forest from San Martín to Junín Depts., 2,600–3,150 m (Fig. 55).

Specimens examined: PERU, HUÁNUCO: Panao, *Macbride 3615* (G, GH, F, K, S, US); Tambo de Vaca, *Macbride 4414* (F, GH); ca. 22 km SE of Huánuco, *Macbride & Featherstone 2081* (F, G, GH, US), *2107* (F, GH, K, US), *2124* (F, GH); Pillao, *Woytkowski et al. 34163* (F, MO, UC, USM). JUNÍN: 68 km W of Satipo to Concepción, *Berry & Aronson 3074* (MO). SAN MARTÍN: valley of Río Apisoncho, ca. 30 km above Jucusbamba, *Hamilton & Holligan 1428* (K, S, UC). WITHOUT LOCALITY: *McLean s.n.* (K).

This species is closely related to *Fuchsia decussata* but has more nodose, funnelform floral tubes, generally shorter petals, longer and more reticulate leaves, and less divaricate branching. Some plants, such as the type collection, have a very striking blue-violet coloration on the leaves and flowers (Fig. 27). This species lacks the green sepal tips of *F. decussata*. It occurs sympatrically with *F. abrupta, F. decussata, F. denticulata,* and *F. sanmartina*.

Around the type locality in Dept. Junín, *F. ferreyrae* is found between 2,650 and 3,100 m. At ca. 2,900 m, it is sympatric with *F. decussata*. Although these two species occur side by side, no intermediate plants could be found. In this area, the two species differ markedly in appearance. *Fuchsia decussata* has flaky, coppery bark and a tight, divaricate branching system with slender, green-tipped flowers. Plants of *F. ferreyrae* are much more floriferous, with broader, more nodose, and totally violet flowers and laxer, simpler branching. In many herbarium specimens, however, it is difficult to distinguish the two species because coloration and leaf texture characters are usually lost upon drying. Several of the specimens cited under *F. ferreyrae* are intermediate with *F. decussata* in certain characters, but are included here because of their noticeably nodose and funnelform floral tubes, larger leaves, or indication of bluish coloration in the foliage. Additional field work is needed in Dept. Huánuco to determine if these species intergrade or if they are always clearly distinct under field conditions, as found at the type locality.

3. **Fuchsia fontinalis** J. F. Macbr., Candollea 8:25. 1940. TYPE: Peru, Dept. Amazonas, Chachapoyas, 1830–1841, *Andrew Mathews* (G-DEL, lectotype, here designated; photograph, MO).

Fuchsia decussata sensu Munz, Proc. Calif. Acad. Sci. IV. 25:56. 1943, pro parte.

Erect to scandent shrubs 0.5–4 m tall with spreading branches. Young growth canescent to densely pilose, often becoming ferrugineous with age; branchlets pilulose to tomentose; older branches 5–12 mm thick with tan, finely fissured bark. Leaves whorled, mostly ternate or quaternate, occasionally opposite, membranous, elliptic to (ob-)lanceolate, acute to attenuate at the base, acute at the apex, 35–110 mm long, 10–35 mm wide, strigillose above and along the veins below, basal leaves noticeably larger than the upper ones; undersurface visibly

reticulate-veined, secondary veins 8–14 on either side of the midvein; margin conspicuously denticulate or serrate. Petioles pubescent, 5–21 mm long, mostly reddish. Stipules filiform, 2–3 mm long, ca. 0.4 mm wide, deciduous to semipersistent. Flowers numerous and generally densely grouped in upper leaf axils or in racemes or many branched terminal panicles; rachis 3–14 cm long with reduced leaves 15–25 mm long subtending the flowers. Pedicels slender, pendant, pubescent, 6–16(–25) mm long. Floral tube subcylindric to narrowly funnelform, 15–28 mm long, 3–4 mm wide and somewhat bulbous at the base, then constricted to ca. 2 mm wide above the nectary and widened gradually above until 4–6 mm wide at the rim, pilose to strigillose outside, glabrous inside. Sepals lanceolate, 10–13 mm long, ca. 3 mm wide, acuminate, spreading-divergent at anthesis. Tube and sepals nitid red or pink. Petals red, usually noticeably shorter than the sepals, lanceolate, 6–9 mm long, 2–3 mm wide, acute, spreading at anthesis. Nectary 4–8-lobed, ca. 1.5 mm high. Filaments pink to red, 9–14 mm and 6–10 mm long; anthers oblong, 2–2.5 mm long, 1–1.5 mm wide, dull white. Style light red, glabrous; stigma capitate, slightly 4-lobed, 1.5–2 mm long and wide, exserted 2–4 mm beyond the anthers. Berry subglobose, 9–10 mm long, 5–9 mm thick, red; seeds tan, 1–1.2 mm long, ca. 0.7 mm wide. Gametic chromosome number $n = 11$.

Distribution: Northern Peru. Shrubs in thickets, banks, and streamsides; endemic to Dept. Amazonas, in upper cloud forest on the E side of the Jalca de Calla-Calla and in the mountains to the east of the Río Utcubamba, 2,900–3,400 m (Fig. 55).

Representative specimens examined: PERU, AMAZONAS: Cerros de Calla-Calla, 18 km SW of Leimebamba (Km 403), *Ambrose 2375* (BH); E side of Calla-Calla, 62 km NE of Balsas, *Berry & Escobar 3608* (MO, USM); Cerro Puma-Urco, 10 km SE of Chachapoyas, *Berry & Escobar 3624* (MO, USM); Leimebamba-La Joya trail, *Boeke 1783* (MO); Leimebamba-Lajasbamba trail, *Boeke 2031* (MO); Cerros Calla-Calla, E side, 18 km above Leimebamba, *Hutchison & Wright 6956* (F, NY, RSA, UC, US, USM); Almirante, *Mathews 1479* (K, OXF); Chachapoyas, *Mathews s.n.* (G-BOIS); Cerro Tinaja, *Ochoa 1653* (F, US); mountains S of Tambo de Ventilla, *Pennell 15794* (PH); Almirante, *Sandeman 59* (F, OXF); upper slopes of Puma Urco, ESE of Chachapoyas, *Wurdack 670* (F, NY, RSA, US, USM); S side of Molinopampa-Diosán pass, *Wurdack 1626* (RSA, US, USM).

This species is allied to *F. decussata* and *F. ferreyrae*. Its flowers are more numerous, however, and are often grouped into definite inflorescences. The leaves are mostly quaternate, unlike the other two species, and the basal leaves are usually considerably larger than the upper leaves.

At its lower altitudinal limit on the eastern slopes of the Jalca de Calla-Calla, *F. fontinalis* is sympatric and forms local hybrids with *F. mathewsii* along pasture borders and stone walls (Fig. 10 and discussion under *F. mathewsii*).

4. **Fuchsia sanctae-rosae** Kuntze, Rev. Gen. 3(2):98. 1898. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):562. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:59, *pl. 9, fig. 48*. 1943. TYPE: Bolivia, Santa Rosa (Department unknown), 1,600 m, 13–20 April 1892, *Otto Kuntze* (NY, holotype). This specimen is in very poor shape, and no intact flowers remain, but the description and locality could only apply to this species.

Fuchsia boliviana Britton, Bull. Torrey Bot. Club 17:214. 1890, hom. illeg., non Carr., 1876. TYPE: Bolivia, Dept. La Paz, Yungas, 1885, *Henry H. Rusby 1813* (NY, holotype; MICH, NY, US, isotypes).

Fuchsia weberbaueri K. Krause, Repert. Spec. Nov. Regni Veg. 1:179. 1905. TYPE: Peru, Dept. Puno, Prov. Sandia, 2,400 m, 1906, *August Weberbauer 661* (B, holotype, destroyed in World War II; photograph, F; G, isotype).

Fuchsia brittonii Johnston, Contr. Gray Herb. 75:39. 1925, nom. nov. pro *F. boliviana* Britton, hom. illeg.

Fuchsia filipes Rusby, Mem. New York Bot. Gar. 7:317. 1927. TYPE: Bolivia, Dept. La Paz, Pulcheri, ca. 3,000 m, 15 July 1921, *Orland E. White 232* (NY, holotype; GH, K, US, isotypes; photographs of GH isotype, NY, RSA).

Erect to scandent, well branched shrubs 1–3 m tall. Branchlets usually subglabrous, occasionally pubescent, purplish red, 2–4 mm thick; older branches 5–18 mm thick with light tan, finely fissured bark. Leaves usually ternate or quaternate, the basal ones much larger than the upper ones, membranous, oblanceolate to (narrowly) elliptic, acute to attenuate at the base, acute to acuminate at the apex, 2–14 cm long, 1–4 cm wide, dark green and glabrous above, paler below (especially when dry) and glabrous except often with pilose hairs along the midrib; secondary veins 6–15 on either side of the midvein, subelevated below; margin subentire to obscurely denticulate. Petiole subglabrous to pubescent, 5–25 mm long, green to red-purple. Stipules lance-linear to narrowly triangular, occasionally connate, 2–4 mm long, 0.5–1.0 mm wide, deciduous. Flowers usually numerous, solitary in upper leaf axils or often appearing loosely racemose or paniculate. Pedicels slender, glabrous, 10–30(–40) mm long, spreading-divergent to drooping. Ovary cylindric, 4–5 mm long, 1–2.5 mm thick. Floral tube subcylindric to narrowly funnelform, 15–22(–27) mm long, 2–3 mm wide at the base, slightly constricted above the nectary and gradually widened above until 4–6 mm wide at the rim, glabrous to sparsely pilose outside, densely pilose inside in lower ⅓. Sepals lance-oblong, acute, 9–13 mm long, 2.5–4 mm wide, rather obtuse-tipped in bud and broader by 1–2 mm than the rim of the tube, spreading-divergent at anthesis. Tube and sepals nitid orange red. Petals orange red, oblong, obtuse to acute, 7–9 mm long, 2–4 mm wide, spreading. Nectary unlobed, ca. 1.5 mm high. Filaments orange red, 6–8 mm and 4–6 mm long; anthers oblong, 2–2.5 mm long, ca. 1.5 mm wide, cream. Style orange red, glabrous; stigma orange red, capitate, slightly 4-lobed, ca. 1.5 mm long and wide, exserted 3–4 mm beyond the anthers. Berry ellipsoid to subglobose, 8–12 mm long, 6–10 mm thick, dark red purple; seeds 1.3–1.6 mm long and 0.8–1.0 mm wide. Gametic chromosome number $n = 11$.

Distribution: Southern Peru and Bolivia. Scattered to locally frequent shrubs in cloud forest from Dept. Cuzco in Peru to Dept. Cochabamba in Bolivia; 1,400–3,000 m (Fig. 55).

Representative specimens examined: PERU, CUZCO: Machupichu, *Balls B6802* (BM, F, K, NA, UC, US); ca. 13 km below Marcapata to Quince Mil, *Berry & Aronson 3019* (MO); Km 170 of Cuzco-Quillabamba road, *Berry & Aronson 3046* (MO); Km 127–128 of Cuzco-Pilcopata road, *Berry et al. 2596* (MO, USM); Km 160 of Cuzco-Paucartambo-Pilcopata road, *Berry et al. 3002* (MO, USM); San Miguel, Urubamba valley, *Cook & Gilbert 1110* (GH, US); Hacienda Santa Rita, Urubamba valley, *Dreyfus s.n.* (USM); above Machupichu on old Inca trail, *Gentry et al. 19384* (MO); Amaybamba, Prov. Convención, *Infantes 6033* (P); Machupichu, *Mexia 8078* (F, G, GH, K, MO, UC); Pillahuata, Cerro de Cusilluyoc, *Pennell 13997* (F, GH, NY, PH, US); between Calca and Hipal, Quebrada de Yanatili, *Raimondi s.n.* (USM); Aguas Calientes, Urubamba valley, *Solomon 3118* (MO); between Pillahuata and Tambomayo, *Vargas 82* (BH, CAS, CUZ, F, MO); Huaillai, Marcapata, *Vargas 1343* (CUZ); Km 75–76 road to Lares, *Vargas 15322* (CUZ); Mant'o, Km 84, *Vargas 15627* (CUZ); valley of Río Tambomayo, *West 7091* (GH, MO, UC). PUNO: Santo Domingo

area, Prov. Sandia, *McCarroll 14* (MICH, NY, S); 2–6 km from Oconeque, Prov. Sandia, *Metcalf 30557* (A, BH, G, MO, UC, US); Ollachea, Prov. Carabaya, *Vargas 6869* (CUZ, RSA); vicinity of Sandia, *Vargas 15151* (CUZ); San Juan de Oro, Prov. Sandia, *Vargas 20604* (CUZ); Agualani-Oconeque, Prov. Sandia, *Vargas 20635* (CUZ). BOLIVIA, COCHABAMBA: Montepunco, 130 km E of Cochabamba, *Adolfo 314* (DS); Incachaca, *Brooke 6693* (F, NY), *6653* (NY); road to Yungas de Tablas, *Cárdenas 6259* (NY, US). LA PAZ: Chulumani, *Albert de Escobar 1303* (TEX); El Chaco, Sur Yungas, *Asplund 1153* (UPS); Unduavi, *Brooke 6610* (BM, F, NY, U); Hacienda Simaco, road to Tipuani, *Buchtien 832* (BM, F, G, K, MO, POM), *5508* (GH, NY, S, US, Z); between Unduavi and Chirca, *Eyerdam 25388* (F, UC); from Puente Villa to Chulumani, *Kelley 1014* (UC); near Ananca, Machacamarca, Prov. Larecaja, *Mandon 624* (BM, F, G, GH, LE, NY, RSA, S, W): Rio Pelechuco, *Williams 2494* (BM, NY); Nequejahuira, Cordillera Real, *Tate 675* (NY); Okara, Cordillera Real, *Tate 912* (NY).

This species can be distinguished from other axillary, short-flowered species by the nearly entire leaves, usually glabrous stems and leaves (except for the pilose midvein below), and the uniformly orange red, nitid flowers. In addition, the stigma is reddish, and the basal leaves are considerably larger than the upper ones. It occurs sympatrically with *F. cochabambana, F. boliviana, F. denticulata, F. furfuracea, F. tincta,* and *F. vargasiana.*

Fuchsia sanctae-rosae has uncommonly wide ecological and altitudinal tolerances. It is found in open, rocky situations such as the ruins of Machupichu or in shady cloud forest thickets. In Dept. Puno, Peru, it occurs on the edges of the town of Ollachea in ditches at 2,700 m; in the neighboring Dept. Cuzco, it occurs as low as 1,400 m, where subtropical floristic elements are already present (Fig. 11).

Beck 1266 (MO; Bolivia, Dept. La Paz, Prov. Murillo, Valley of Zongo at 2,170 m, 10 km from Cahua towards La Paz) is a probable hybrid with *F. denticulata.* This specimen has the stout stems and firm, elliptic leaves of *F. denticulata,* but the flowers are characteristic of *F. sanctae-rosae,* except for the intermediate tube length. The pollen stainability is 63% of 500 grains. Probable hybrids with *F. furfuracea* and *F. tincta* are discussed under those respective species.

5. Fuchsia loxensis Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 6:106, *t. 536, figs. 1–5.* 1823. Munz, Proc. Calif. Acad. Sci. IV. 25:28, *pl. 2, fig. 14.* 1943; Opera Bot., Ser. B, 3:18. 1974. TYPE: Ecuador, Prov. Loja, near Loja, ca. 2,000 m, July–Aug. 1802, *Alexander von Humboldt & Aimé Bonpland* (P HBK. Herb., holotype, not seen; photograph, F; microfiche, MO).

Fuchsia umbrosa Bentham, Pl. Hartw. 176. 1845. TYPE: Ecuador, Prov. Pichincha, Hacienda de Pinantura, near Quito, 1841–1843, *Theodor Hartweg 983* (K Bentham Herb., holotype; BM, BR, CGE 2 sheets, G, K Hooker Herb., LE, OXF, W, isotypes).

Fuchsia apiculata I. M. Johnston, Contr. Gray Herb. 75:34. 1925. TYPE: Ecuador, Prov. Azuay and Cañar, between Cuenca and Huigra, 2,700–3,300 m, 12–13 Sept. 1923, *Albert S. Hitchcock 21667* (GH, holotype; photograph, UC; NY, US, isotypes).

Fuchsia hypoleuca I. M. Johnston, Contr. Gray Herb. 75:34. 1925. TYPE: Ecuador, Prov. Loja, between Loja and San Lucas, 2,100–2,600 m, 6 Sept. 1923, *Albert S. Hitchcock 21440* (GH, holotype; photograph, UC; NY, US, isotypes). Munz, Proc. Calif. Acad. Sci. IV. 25:57, *pl. 8, fig. 45.* 1943; Opera Bot., Ser. B, 3:17. 1974.

Scandent to mostly erect shrubs or small trees (1–)1.5–6 m tall, usually densely branched. Young growth canescent to finely pilose; older stems 8–25(–40) mm thick, with flaky, tan bark. Leaves ternate or quaternate, membranous, (narrowly)

elliptic to oblanceolate, acute to narrowly cuneate or subrounded at the base, acute to acuminate at the apex, 2–9(–13) cm long, 0.8–3(–4) cm wide, medium to dark green and subglabrous to strigose above, pale green and strigose-pilose below, especially along the veins; secondary veins (5–)6–10(–13) on either side of the midvein; margin (sub-)denticulate. Petioles mostly strigose, 7–15(–17) mm long. Stipules narrowly lanceolate, 2–4 mm long, ca. 1 mm wide, subpersistent. Flowers few to numerous and solitary in leaf axils. Pedicels drooping, 8–23(–32) mm long. Ovary ellipsoid to cylindric, 5–8 mm long, 1.5–2.5 mm thick. Floral tube narrowly funnelform, (15–)19–30(–33) mm long, 2–3(–4) mm wide and slightly bulbous at the base, then narrowed to 1.5–2.5 mm above the nectary and gradually widened above until 5–8 mm wide at the rim, sparsely strigose outside, pilose in lower ⅓ inside. Sepals ovate-lanceolate to lanceolate, 9–16 mm long, 3–5 mm wide, acute, spreading to strongly divergent or slightly reflexed at anthesis. Tube and sepals bright scarlet. Petals dull scarlet, oblong-elliptic to subrotund, 6–10(–11) mm long, (2–)3–8 mm wide, acute to rounded at the apex. Nectary mostly unlobed, ca. 1 mm high. Filaments red, 5–10 mm and 4–7 mm long; anthers oblong, 2–2.5 mm long, ca. 1.5 mm wide, white. Style red, pilose in lower ½–⅓; stigma capitate, 4-cleft at the apex, 1.5–2.5 mm long, 1–2.5 mm wide, cream to scarlet. Berry ellipsoid, 4-angled before maturity, 13–18 mm long, 7–10 mm thick, red purple when ripe; seeds 1.5–2 mm long, ca. 0.8 mm wide. Gametic chromosome number $n = 11$.

Distribution: Ecuadorian Andes. Locally common in hedgerows along fields and in thickets, mainly in the moderately dry interandean valleys of Ecuador, also on the moister eastern and western slopes, from Loja to Pichincha, with a few scattered collections farther north in Imbabura and Carchi, (2,000–)2,500–3,500(–3,800) m (Fig. 56).

Representative specimens examined: ECUADOR, AZUAY: 13 km from Cuenca past Sayausí, *Berry & Escobar 3185* (MO, QCA); along Río Yanucay above San Joaquín, *Berry & Escobar 3210* (MO); along Río Matadero W of Cuenca, *Camp E-1914* (NY, RSA, US); Sayausí, *Harling 1396* (NY, S); Tambolama and Huasi-huaico, W of Cuenca, *Lehmann 4595* (K). BOLIVAR: Chaparro de Gualicón, Loma, Cordillera Occidental, *Acosta Solis 6268* (F); Urcu-corral Chillanes, *Acosta Solis 6624* (F); Pucará de Telimbela, Cordillera Occidental, *Acosta Solis 6818* (F); Alto de Telimbela, *Acosta Solis* 7154 (F); Balsapampa to San Miguel, *Harling et al. 9531* (RSA). CAÑAR: near Pimo, *Camp E-4135* G, MO, NY, P, RSA, S, UC, VEN); between Cuenca and Huigra, *Hitchcock 21688* (US); Ventanillas, above Shoray, E slope of Cerro Yanguang, 34 km ENE of Azogues, *Fosberg & Prieto 22775* (RSA, US); between Tambo and Sucsal, *Giler* (*Camp number*) *E-2756* (NY, RSA). CARCHI: Páramos de El Angel, *Benoist 3637* (P). CHIMBORAZO: Sibambe, Hacienda La Carmela, sección Era-Pata, Cordillera Occidental, *Acosta Solis 5432* (F); road from Pusucucho to El Placer, Cordillera Oriental, *Acosta Solis 7253* (F); road from Chambo to Sanguay, *Albert de Escobar 1091* (TEX); near Quinacorral, *André in 1876* (K); slopes of Cerro Chiguazo, *Lugo 512* (RSA); Javiñac, ca. 15 km from Panipe, *Lugo 519* (RSA); ca. 3–4 km from Puela, *Lugo 576* (RSA); Chontapamba, between Puela and Baños, *Lugo 741* (RSA); Manzano, 1 km from Puela, *Lugo 1303* (RSA); between Baños and Riobamba, *Lugo 1844* (RSA); between Guaranda and Bodegas, *Remy in 1836* (P); vicinity of Huigra, Hacienda de Licay, *Rose 22477* (US); road Riobamba-Huamboya, *Scolnik 1533* (RSA); Pallatanga, *Spruce 5798* (BM, CGE, G, K 2 sheets, NY, OXF, TCD, W); Hacienda Joyagshi, road from Sibambe to Tambo, *Wiggins 10705* (POM). COTOPAXI; San Miguel, *André 4015* (K); Pilaló, *Harling 4877* (LL, NY, S); from Pilaló to Macuchi, *Haught 2955* (POM, US); Pilaló, *Holm-Nielsen & Jeppesen 1141* (AAU, S); Panamerican highway, ca. 6 km N of Lasso, ENE of Pastocalle, *Sparre 15805* (S). IMBABURA: Páramo de Cotacachi, from Otavalo to Apuela, *Davis 276* (MO); Mojanda, *Sodiro in 1903* (P). LOJA: Cisne, *André s.n.* (K); Loja, *André s.n.* (K); between Saraguro and San Lucas, *Asplund 17973* (NY, S); 5 km S of Saraguro, *Berry & Escobar 3192* (MO); 11 km S of Saraguro, *Berry & Escobar 3196* (MO); Cerro Villonaco, *Berry & Escobar 3204* (MO), *Camp E-238* (NY, RSA); Cerros de Acacana, ca. 30 km N of Loja,

Espinosa E-1440 (POM, RSA); mountains of Loja, *Hartweg 733* (BM, CGE, G, K, LE, NY, OXF, P, W); Km 43 on Panamerican highway N of Loja, *Holm-Nielsen 4708* (AAU, MO, NY, S); San Lucas, *Jameson 170* (K); Santiago, *Poortman 151* (P); Cerro Villonaco, 20 km W of Loja, *Sparre 16244* (S). PICHINCHA: Gualilagua, El Corazón, *Acosta Solis 7110* (F); Valle Seco del Pedregal, *Acosta Solis 8442* (F); near Tambillo, *André 3681* (K); Páramo de Paguangualli, Corazón, *André in 1876* (K); Machachi, *Asplund 6226* (S); Páramos de Aloag, *Benoist 3060* (P, RSA); N of Volcán Cotopaxi on Panamerican highway, *Berry & Escobar 3233* (MO, QCA); INIAP station, 14 km S of Quito, *Escobar 621* (MO); ascent to Cotopaxi, *Espinosa E-2342* (RSA); between Tambillo and Aloag, 28 km S of Quito, *Fosberg 22549* (COL, NY, RSA, US); road Quito to Santo Domingo de los Colorados, near top of cordillera, *Gentry 9470* (MO, S); vicinity of Tambillo, *Penland & Summers 959* (F, GH, POM, RSA); pass at Páramo el Corazón, *Prescott 922* (DS, NY); near Quito, *Sodiro in 1898* (P); road to Iliniza, *Sparre 15785* (S); Panamerican highway, ca. 1 km N of RR, ESE of El Chaupi, *Sparre 15801* (S). TUNGURAHUA: between Leito and La Cima, *Acosta Solis 9024* (F); between Huambaló and Cotaló, *Acosta Solis 9717* (F); between La Cima and Riochico, *Acosta Solis 10234* (F); Hacienda Yanayacu, Mocha, *Balls B7188* (F, K, UC, US); near Agua de Oro, W of Ambato, *Heinrichs 828* (G, NY, Z); Mocha, *Laudeman 35* (BM); Runtún, ca. 4 km from Baños, *Lugo 1190* (MO, RSA); Cusatagua, near Ambato, *Pachano 217* (NY, US); S of Baños, *Penland & Summers 93* (BH, F, POM); near Baños, *Spruce 5203* (BM, CGE, G, GH, K, LE, NY, OXF, P, TCD, W). ZAMORA-CHINCHIPE: Km 12–14 road from Loja to Zamora, *Dodson & Thien 1369* (DS, MO).

Fuchsia loxensis is distinguished from other axillary, short-flowered species in the following combination of characters: leaves ternate or quaternate, elliptic to subrotund petals, 4-angled ovaries, and a generally erect, shrubby to arborescent habit. Although it has been placed in its own species group with two other short-flowered, but rather distantly related species, the leaves and flower shape resemble some of the long-tubed members of the *F. petiolaris* species group such as *F. ampliata*. It occurs sympatrically with *F. ampliata*, *F. harlingii*, and *F. vulcanica*.

As treated here, *F. loxensis* is a wide ranging and variable species including all the short-tubed, strictly axillary-flowered collections of *Fuchsia* in Ecuador except for *F. scabriuscula* and *F. steyermarkii*. The shape of the leaves, petals, and floral tubes as well as pubescence are characters that vary widely in this complex. The plant habit and habitat are important characters that, unfortunately, are too little known for most collections because detailed field observations have not been made. Plants that I have seen in Pichincha and Azuay were large, erect shrubs with thick basal stems and often grew in hedgerows. Plants in northern Loja were more sprawling in thickets, as is more typical in the section. There are too few critical field observations in this group, and further study may lead to the recognition of additional taxa. Some of the different geographical variants found are:

The Central Valley in Pichincha, Cotopaxi, Tungurahua, and Azuay. Collections from these areas are from high elevations (over 3,200 m in the north and above 2,800 m in the south) and are generally from erect, hedgerow shrubs. The habitats in these areas are somewhat drier than most fuchsias tolerate. The type of *F. umbrosa* has rather long, ampliate floral tubes (31–33 mm long), sepals 16 mm long, and broad leaves, but it comes from the Central Valley southeast of Quito and may just be a robust shade plant of *F. loxensis*.

Imbabura. The two specimens from this province grow at high elevations (ca. 3,400 m) but have unusually short floral tubes (ca. 15 mm long), oblong petals, and thin, ternate leaves with narrowly cuneate to attenuate leaf bases. This might be a new or different species, but more material is needed.

Bolivar and western Cotopaxi. Collections from the western slopes of the

Andes in these provinces grow at considerably lower elevations (2,400–2,800 m) than the previous groups, and they often have larger leaves and flowers. No living plants of these entities were seen, and there might be some intergradation with *F. ampliata*.

Northern Loja. Local populations occurring between Saraguro and San Lucas have an unusual white leaf undersurface and until now have been recognized as a separate species, *F. hypoleuca*. As noted in the original publication of that species (Johnston, 1925) however, it is an associated fungus with a thick layer of whitish mycelia, not the plant's own pubescence, that causes the unusual leaf characteristic. In the mass of mycelia and epidermal trichomes that one finds together on the leaf undersides, stalked structures called "brown caps" by D. B. O. Savile (pers. comm.) are often observed, and anatomical sections show that these are definitely part of the fungus and not glandular processes of the plant epidermis (R. Keating, pers. comm.). Fungal specimens sent to a specialist for examination were apparently sterile and could not be identified (D. B. O. Savile, pers. comm.). Wider sampling of *Fuchsia* populations in Loja and further evaluation of this fungal relationship will be necessary before the relationships of these northern Loja populations with others of *F. loxensis* can be confirmed, however.

Tungurahua and Cañar. The set of collections labelled *Spruce 5203* probably is a mixture of *F. loxensis* (sheets at BM, CGE, NY, and OXF), while others (G, GH, and P) have nitid, dentate leaves and floral tubes ca. 35 mm long. The lack of any specific locality information makes evaluation of these specimens difficult.

Hitchcock 21667 (GH, NY, US), from the Azuay-Cañar border area, was described as *F. apiculata*, but its buds are no more pointed than other collections throughout the range of this complex, and no other distinguishing characters are apparent.

6. **Fuchsia scabriuscula** Bentham, Pl. Hartw. 177. 1845. Munz, Proc. Calif. Acad. Sci. IV. 25:58, *pl. 8, fig. 46*. 1943; Opera Bot., Ser. B, 3:22. 1974. TYPE: Ecuador, Prov. Pichincha, W slopes of the Quito Andes, Oct. 1843, *Theodor Hartweg 987* (K Bentham Herb., holotype; photograph, MO; BM, BREM, CGE, G, K Hooker Herb., OXF, isotypes; photograph of B isotype, POM). Fig. 22.

Decumbent to erect shrubs 0.5–2.5 m tall. Branchlets subterete, 2–5 mm thick, pilose-hispidulous with suberect, whitish hairs; older branches with tan, exfoliating bark. Leaves opposite, very rarely ternate, membranous, with finely reticulate, rugulose venation, elliptic to slightly ovate, acute to rounded at the base, acute to acuminate at the apex, 2.5–12(–14) cm long, 1.5–5(–6) cm wide, dull green and strigose above, pale green to flushed purple and strigose below, especially along the veins; secondary veins 8–14 on either side of the midvein, subelevated below; margin subentire. Petioles densely pilose, 5–25 mm long. Stipules lance-linear, 2–3.5 mm long, thick at the base, terminating in a long, dark, filiform tip, subpersistent. Flowers few and solitary in upper leaf axils. Pedicels divergent to drooping, pilose, 10–25 mm long. Ovary oblong, 5–6 mm long, 2–3 mm thick, strigose to hispidulous, green. Floral tube narrowly funnel-

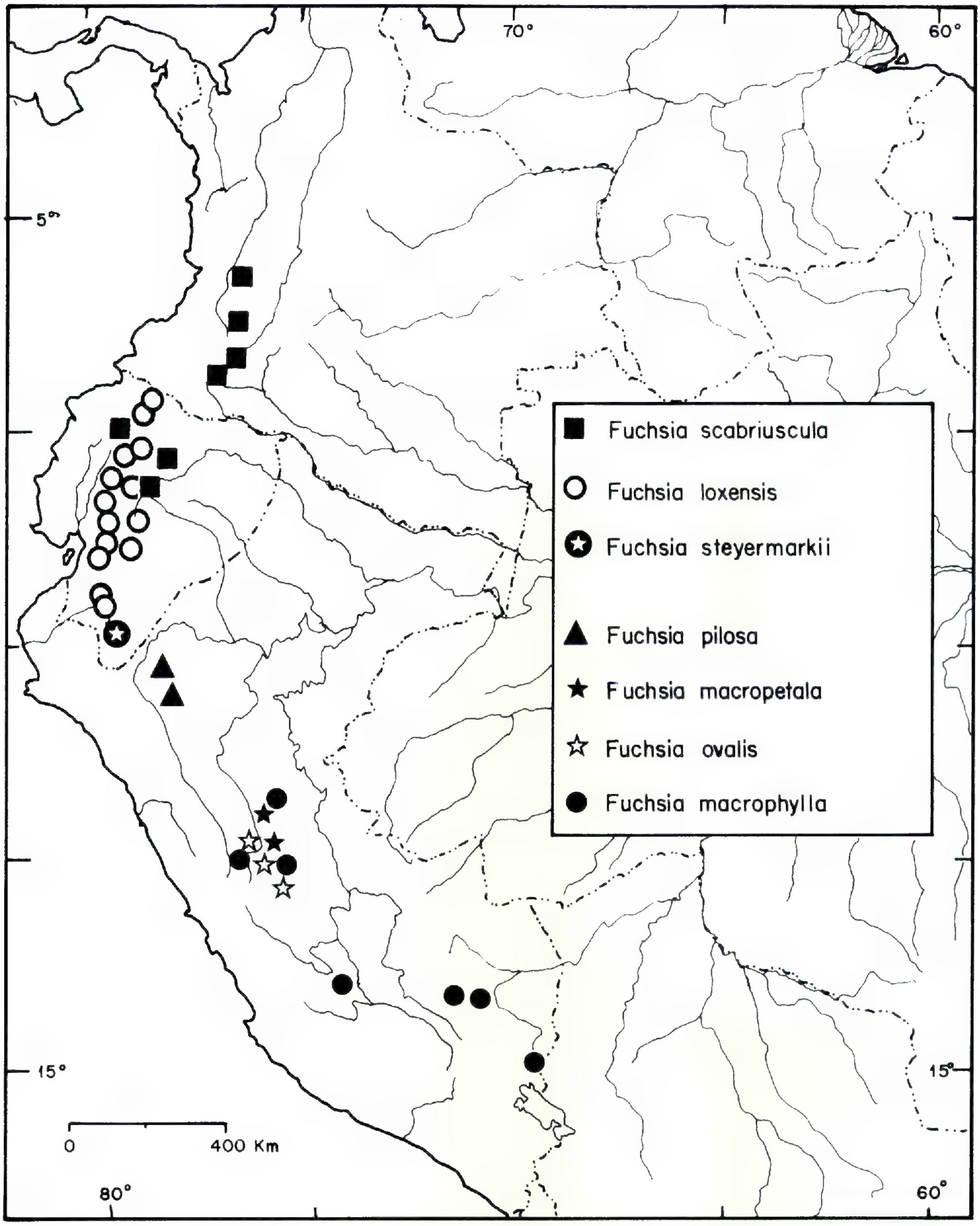


FIGURE 56. Distribution of the *Fuchsia loxenis* and *F. macrophylla* species groups.

form, 15–27 mm long, 2–3 mm wide at the base, slightly narrowed to 1.5–2.5 mm wide above the nectary and gradually widened above until 5–7 mm wide at the rim, strigose to hispidulous outside, densely pilose inside in lower ½. Sepals lanceolate, 9–12 mm long, 3–4 mm wide, acuminate, tips mostly free in bud, spreading at anthesis. Tube and sepals whitish pink to red. Petals pink to scarlet, elliptic-oblong, 7–10 mm long, 3–4.5 mm wide, broadly acute to rounded at the apex, spreading at anthesis. Nectary usually unlobed, green, ca. 1.5 mm high.

Filaments red to pink, 5–7 mm and 3–5 mm long; anthers elliptic-oblong, 1.5–2 mm long, ca. 1 mm wide, bright white. Style densely villous for most its length, pink; stigma subglobose, 4-cleft at the apex, ca. 2 mm long and ca. 2 mm wide, exserted 1–4 mm beyond the anthers, white. Berry oblong before maturity, becoming subglobose when ripe, usually deep, nitid purple; seeds tan to bright purple, 1–1.3 mm long, 0.8–1.0 mm wide.

Distribution: Ecuador and southern Colombia. Low shrubs locally frequent in clearings, thickets, and moist banks of cloud forest; in Ecuador, in Napo, Pichincha, and Tungurahua Provinces, on both the east and west slopes of the Andes; in Colombia, on the eastern slopes of the Nudo de Pasto in Putumayo, in the Cordillera Central as far north as Valle, and in the Cordillera Oriental to the Cauca-Huila border; 1,400–2,750 m (Fig. 56).

Representative specimens examined: COLOMBIA, CAUCA: Km 31–32 from Pitalito toward Mocoa, *Berry 3596* (COL, MO); Río Villalobos, vicinity of Río Suazita, *Schultes & Villarreal 5173* (COL, F, GH). HUILA: Km 25 of Pitalito-Mocoa road, *Berry 3593* (COL, MO); Km 28–32 of road from Pitalito to Mocoa, *Luteyn et al. 7550* (COL, MO, NY); La Plata, *von Sneidern 2462* (S). PUTUMAYO: Mirador, between San Francisco and Mocoa, *Bristol 545* (GH); Río Susunga, 18–20 km W of Mocoa, *Fosberg 20395* (NY, RSA, UC, US); Km 90–91 between Sibundoy and Mocoa, *Luteyn et al. 5041* (COL, MO); Los Monos, Km 92 between San Francisco and Mocoa, *Plowman & Davis 4328* (COL). VALLE: El Guayabo, from Palmira to Taco, *Berry & Escobar 3565* (COL, MO). ECUADOR, NAPO: Río Chingual, *Acosta Solis 13250* (F); Cuyuja, *Balslev & Madsen 10476* (AAU, MO); between Baeza and Papallacta, *Mexia 7339* (GH, NA, S, UC, US); Baeza to Tena, ca. 5 km S of Cosanga, *Øllgaard & Balslev 10248* (AAU, MO); above Baeza on road to Quito, *Plowman et al. 3889* (COL, F, GH, K). PICHINCHA: Guaruna, Km 38 of road to Saloya, *Acosta Solis 11018* (F); Mindo, *André in 1876* (K); Corazón, towards Miligalli, *André 3710* (K, NY); Salvador, below San Juan, *Asplund 16184* (NY, S); 34 km W of Chillogallo towards Chiriboga, *Berry & Escobar 3243* (MO, QCA); 30 km W of Cotocallao towards Nanegal, *Berry & Escobar 3178* (MO, QCA); W slope Cerro Corazón, *Camp E-1663* (NY, RSA); Quito-Santo Domingo road, *Haught 3224* (A, BH, US); Quito Andes, *Jameson 92* (BM, G, GH, P); Quito-Nono-Puerto Quito road, 13 km NW of Nono, *Luteyn et al. 6519* (MO, NY); road Nono-Tandayapi, Km 43–45 along Río Alambí, *Sparre 15989* (S). TUNGURAHUA: Baños, *Benoist 4223* (P); Río Verde, *Harling et al. 10159* (MO, RSA); valley of Río Pastaza, between Baños and Cashurco, *Hitchcock 21781* (GH, NY); Montaña Woma, 11 km E of Baños, *Holm-Nielsen & Jeppesen 279* (AAU, DS); Volcán Tungurahua, *Lehmann 4995* (F, K). WITHOUT LOCALITY: *Spruce 5038* (BM, CGE, G 2 sheets, GH, F, K, LE, NY, OXF, S 2 sheets, TCD, W 3 sheets).

This species is easily distinguished by its finely rugulose, opposite leaves and stiff, whitish pubescence on most parts. Just a few flowers are borne on each branch; these later produce round, dark purple berries. *Fuchsia scabriuscula* occurs sympatrically with *F. cuatrecasasii, F. hartwegii, F. macrostigma, F. orientalis, F. pallescens, F. sessilifolia, F. sylvatica,* and *F. verrucosa.* No hybrids have been detected with these species, despite close examination of several populations.

7. **Fuchsia steyermarkii** P. Berry, **sp. nov.** TYPE: Ecuador, Prov. Zamora-Chinchipe, between Rancho Achupallas and Tambo Valladolid, deep forest along the W side of Río Valladolid to Río Molino, 1,800–2,000 m, 12 Oct. 1943, *Julian A. Steyermark 54596* (NY, holotype; photograph, MO).

Frutex pilosus ramosissimus ca. 2 m altus. Folia linearia, revoluta, opposita vel 3–4-verticillata sed plerumque fasciculata, firme membranacea ambis extremis acuta, 20–70 mm longa, 2–3 mm lata, superne subnitida atroviridia strigosaque, subtus pallidioria praesertim in costa media margineque dense pilosa; nervis secundariis plerumque inconspicuis, margine valde revoluta; petiolis 0.2–2.0 mm

longis; stipulis fuscatis, lanceolato-linearibus, ca. 1.5 mm longis, subpersistentibus. Flores pauci, axillares, ad apicem ramorum dispositi; pedicellis 16–18 mm longis; ovario oblongo, 4–5 mm longo. Tubi florales roseo-rubri, anguste infundibuliformes, 33–37 mm longi, basi 2.5–3 mm lati et bulbosi inde ca. 2 mm lati constricti superne gradatim dilatati summo 5–6 mm lati, extus laxe strigoso-pilosi, intus infra medium pilosi. Sepala lanceolata, acuminata, 13–15 mm longa, 3–4 mm lata, roseo-rubra. Petala coccinea, lanceolata, acuta vel subacuminata, 9–10 mm longa, ca. 3 mm lata. Filamenta antisepala 8–9 mm longa antipetala 6–7 mm longa, antheris oblongis, 2.5–3 mm longis ca. 2 mm latis. Stylus laxe villosus, stigmate capitato apice leviter 4-fisso, ca. 2 mm longo, 2–3 mm lato. Bacca matura non visa.

Densely pilose, many-branched shrub ca. 2 m tall. Branchlets subterete, 1.5–4 mm thick, pilose, with copper-colored bark. Leaves opposite to quaternate but usually appearing fasciculate due to the very reduced lateral shoots, firmly membranous, linear, acute at both ends; 20–70 mm long, 2–3 mm wide, subglossy dark green and sparsely strigose above, pale and densely pilose below along central nerve and margin; secondary veins mostly inconspicuous, midvein strongly prominent below, margin strongly revolute. Petioles 0.2–2 mm long. Stipules dark, lance-linear, ca. 1.5 mm long, subpersistent. Flowers few and axillary near the branch tips. Pedicels 16–18 mm long. Ovary oblong, 4–5 mm and ca. 2 mm thick. Floral tube narrowly funnelform, 33–37 mm long, 2.5–3 mm wide and bulbous at the base, narrowed to ca. 2 mm wide above the nectary and gradually widened above until 5–6 mm wide at the rim, loosely strigose-pilose outside, pilose inside in lower ½. Sepals lanceolate, acuminate, 13–15 mm long, 3–4 mm wide. Tube and sepals rose red. Petals scarlet, lanceolate, acute to subacuminate at the apex, 9–10 mm long, ca. 3 mm wide. Nectary unlobed, ca. 1.5 mm high. Filaments red, 8–9 mm and 6–7 mm long; anthers oblong, 2.5–3 mm long and ca. 2 mm wide, cream yellow. Style red, loosely villous for most of its length; stigma capitate, slightly 4-lobed at the apex, 2 mm long, 2–3 mm wide, exserted 1–3 mm beyond the anthers. Berry not seen.

Distribution: Known only from the type locality on the eastern slopes of the Andes in southernmost Ecuador (Fig. 56).

This is an unmistakable species because of its linear, revolute leaves and dense, pilose pubescence. It comes from a very poorly known area of Ecuador that is still accessible only by foot or by mule. Further collections would be desirable to determine the extent of variability in leaf shape and the probable affinities of this species. It is named in honor of Dr. Julian Steyermark, undoubtedly the foremost neotropical plant collector of this century.

8. Fuchsia nigricans Linden ex Planchon, Fl. Serres Jard. Eur. 5: *t. 481.* 1849. TYPE: Venezuela, Edo. Mérida, between Mendoza and Timotes, entrance to Paramillo de la Mucutí, 2,270–2,600 m, 1843, *Jean Jules Linden 368* (P, holotype; BM, G 2 sheets, K, LE, TCD 2 sheets, US, W 2 sheets, isotypes). This same collection number at OXF was used as the type for *F. caracasensis* Fielding & Gardner, Sert. Pl. *t. 29.* 1844; that specimen is different from those listed above, however, and is a natural hybrid of *F. nigricans* and *F. gehrigeri* (see discussion on p. 43). Most of these collections have printed localities on the labels such as "Caracas" or "entre Caracas et Mérida," but the actual locality is given by Linden in the protologue. Fig. 21.

Fuchsia atrorubra I. M. Johnston, Contr. Gray Herb. 75:31. 1925. TYPE: Colombia, Dept. Risaralda (formerly Caldas), Santa Elena, above Santuario, 2,000–2,300 m, 7–13 Sept. 1922, *Francis W. Pennell 10313* (GH, holotype; NY, isotype).

Fuchsia sylvatica sensu Munz, Proc. Calif. Acad. Sci. IV. 25:68, *pl. 11, fig. 58.* 1943, pro parte.

Fuchsia adpressipilis Steyermark, Fieldiana Bot. 28:438. 1952. TYPE: Venezuela, Edo. Lara, between Santo Domingo and Los Quebraditos, S of Las Sabanetas, above Humocaro Bajo, 2,439–2,475 m, 8 Feb. 1944, *Julian A. Steyermark 55381* (F, holotype; NY, isotype).

Erect to scandent shrubs 1–3 m tall with suberect to spreading branches. Young growth densely canescent with appressed or less often suberect hairs; branchlets terete, 2–5 mm thick, dull purple to light green; older branches with light brown, splitting bark. Leaves mostly ternate, opposite or rarely quaternate, membranous, smooth to sulcate nerved, mostly elliptic or obovate, but also spatulate or subpanduriform, acute to attenuate or cuneate at the base and sometimes noticeably unequal, acute to rounded at the apex, (4–)7–15(–18) cm long, (2–)3–8(–9) cm wide, medium-dark green and strigillose to subglabrous above, pale green and strigillose below, especially along the veins; secondary veins 11–16(–20) on either side of the midvein, sometimes red tinged; margin remotely gland-denticulate. Petioles strigillose, 12–35(–48) mm long. Stipules narrowly triangular, dark purple, 1–2 mm long, ca. 0.8 mm wide, succulent at the base, subulate at the apex, subpersistent. Flowers few to numerous, axillary in upper leaf nodes or in terminal bracteate racemes; rachis 4–22 cm long; bracts narrowly elliptic, short petiolate, loosely spaced. Pedicels slender, 3–9 mm long, suberect in bud to divergent or drooping at anthesis. Ovary narrowly cylindric-fusiform, densely canescent or strigillose, 6–11 mm long, 2–3 mm thick. Floral tube subcylindric, 14–22 mm long, 1.5–3 mm wide and slightly bulbous at the base, gradually widened above until 3–5(–6) mm wide at the rim, canescent-strigillose outside, densely pilose inside in lower ½. Sepals lanceolate, acute, 6–10 mm long, 3–4 mm wide, spreading at anthesis. Tube and sepals pale pink to lavender or light red. Petals much darker, generally dark purple, narrowly elliptic-oblong, acute, 5–10 mm long, 2–3.5 mm wide, suberect to spreading at anthesis. Nectary green, shallowly 4-lobed, ca. 1.5 mm high. Filaments deep purple, 5–6 mm and 3–4 mm long; anthers oblong, 1.5–2 mm long, ca. 1 mm wide, dull white. Style glabrous, pink to purple; stigma capitate, subtetragonous, 2–3 mm long, 2–3.5 mm wide, 4-lobed in upper ½, pink, slightly exserted beyond the anthers or in contact with the antesepalous stamens at anthesis. Berry cylindric, 15–25 mm long, 6–10 mm thick, dull green to flushed purple, strigillose, slightly verrucose before maturity; seeds tan, 1.3–1.6 mm long, ca. 0.8 mm wide. Gametic chromosome number $n = 11$.

Distribution: Venezuela and Colombia. Scattered to locally frequent shrubs in forest openings, streambanks, along roadsides, and in moist thickets in mid-elevation cloud forest; in Venezuela, from Lara to Táchira at 2,100–2,650 m; in Colombia, in all three cordilleras: in the Cordillera Oriental known only from Norte de Santander near the Venezuelan border; in the Cordillera Central in Tolima, Quindío, Caldas, and Antioquia; in the Cordillera Occidental from Antioquia south to Cauca; 1,700–2,700 m (Fig. 57).

Representative specimens examined: VENEZUELA, LARA: below La Sabaneta, 15 km from Los Naranjos above Humocaro Bajo, *Berry & Azuaje 2500* (MERF, MO); trail from Humocaro to Buenos Aires, below Páramo de Las Rosas, *Liesner et al. 8001* (MO), *8215* (MO, VEN). MÉRIDA: La Culata

to El Valle, *Badillo 5587* (MY); between El Morro and Aricagua, Loma de la Vagabunda, *Badillo 6567* (MY); Guaraque to Tovar, *Benitez de Rojas 2076* (MY); La Mosquera, Mucuquí, above Pueblo Nuevo, *Bernardi 232* (NY); Monte Zerpa, *Bernardi 653* (NY); 10 km above La Azulita to La Carbonera, *Berry & Centeno 2513* (MER, MERF, MO); 1 km below Chachopo on road to Timotes, *Berry 3131* (MO, VEN); 4 km below San Eusebio to La Azulita, *Berry 3454* (MO, VEN); La Carbonera, *Berry 3451* (MO); between La Mucuy and Mesa de los Pinos, *Berry 3438* (MO, VEN); Páramo de la Sal, *Jahn 507* (VEN); above Palmira, *Jahn 509* (US, VEN); Páramo de Aricagua, *Jahn 1028* (US, VEN); road to El Morro, *Jahn in 1910* (VEN); El Filo, between Guaraque and Tovar, *López-Palacios 8* (MER); trail from La Escalera to Puente de La Escalera, *Luteyn et al. 6208* (MO); road to Páramo de los Colorados, *Quintero et al. 1280* (MER); El Chorotal, *Quintero 1616* (MER); Tienditas del Chama to Aricagua, *Quintero & Ricardi 1772* (MER); between El Chorrerón and La Cueva, road to Páramo de Palmira, Dpto. Miranda, *Ruiz-Terán & Dugarte 12493* (MERF); Quebrada La Honda, E of Los Nevados, Dpto. Libertador, *Ruiz-Terán 12090* (MO); between Los Corales and Los Cuadros, *Steyermark 55769* (F, US); 2 km above Las Tapias, S of Bailadores, *Tillett & Hönig 738-465* (MO, VEN); road from Manzano Alto to Páramo de los Conejos, ca. 7 km NE of Mérida, *Wessels-Boer 2245* (MER, MO, U). TÁCHIRA: 13 km E of El Portachuelo, road to Pregonero, *Berry 3288* (MO, VEN); 2 km E of Zumbador, road to Queniquea, *Berry 3294* (MO, VEN); 15 km E of Zumbador to Queniquea, *Berry 3304* (MO, VEN); between Zumbador and San Isidro, *Bunting 2548* (GH, MY); Páramo el Pantano, *Charpin et al. 13446* (G); Quebrada Agua Azul, S of El Reposo, *Steyermark & Liesner 118431* (MO, VEN). TRUJILLO: Campo Elías to Boconó, *Badillo 4965* (MY); 12 km W of San Rafael, old road Boconó-Trujillo, *Berry 3103* (MO, VEN), *3104* (MO, VEN); 5 km above La Mesa de Esnujaque, road to Dury, *Berry 3130* (MO); 8 km W of El Batatal to Boconó, *Berry 3093* (MO, VEN); *3095* (MO, VEN); Agua Obispo, *Funck & Schlim 797* (BM, CGE, F, G, LE, OXF, P 2 sheets, W); Río de Agua Negra, near Boconó, *Lasser 1175* (US, VEN); Misisí, slopes of Páramo de la Cristalina, *Ruiz-Terán & López-Palacios 7635* (MERF, MO); Páramo de Guaramacal, 15 km from Boconó, *Ruiz-Terán 9224* (MERF, MO). COLOMBIA, ANTIOQUIA: Santa Elena, *Archer 1195* (US 2 sheets); near Nariño, *Barkley & Johnson 180826* (COL, RSA, US). CALDAS: Mt. Cardal, *Tracey 344* (K). CHOCÓ: N of Albán, *Dugand & Jaramillo 3040* (COL, US); Quebrada El Sucio above Carmen de Atrato, *Fosberg & Core 21550* (RSA, S, US). NORTE DE SANTANDER: Ocaña to Pamplona, *Kalbreyer/Sisale 1104* (K); Prov. of Ocaña, *Schlim 338* (P). QUINDÍO: Río Santa Rita, Salento, *Killip & Hazen 8966* (GH, NY, PH, US); Río Quindío, Salento, *Pennell 10099* (GH): Salento, *Pennell & Hazen 10144* (GH, NY, PH, US). TOLIMA: Alto San Juan-Quindío, *André 2072* (K); Quindío, *André s.n.* (K); La Suiza, above Ibagué, *Cuatrecasas 3260* (MA); Las Juntas, Combayeque, *Goudot 3* (P); Río Toche to Machín, *Killip & Hazen 9564* (GH); Rio Combeina, Juntas, *Schneider 1156* (COL, S); Toche, *von Sneidern 3090* (COL, S); la Mediación, Quindío, *Triana 3811* (G, K, W). VALLE: above Las Brisas, between El Tabor and Alto de Mira, *Cuatrecasas 22425* (F, RSA, VALLE).

This species is vicarious with *Fuchsia sylvatica,* which differs in a series of minor characters such as lighter colored petals, narrower fruits, more rugulose leaves, and denser, more cordate bracts. They are geographically separated by the Río Patía valley in the Cordillera Occidental of southern Colombia. The pattern of distribution of these two species suggests a northern origin in the Cordillera Oriental of Colombia and Venezuela, where *F. nigricans* is now most common and widespread. As with at least three other species in the section, it may have spread westwards into the Cordillera Central and Cordillera Occidental; *F. nigricans* is not found south of 3°N Latitude or in the Nudo de Pasto area. *Fuchsia sylvatica* may have diverged secondarily south of the Patía barrier, where it is now restricted on the western slopes of the Cordillera Occidental in Ecuador. If a northwards migration route had been used, one would expect to find members of these species in the Nudo de Pasto or in the southern parts of the Colombian cordilleras, but this is not the case.

Fuchsia nigricans and *F. sylvatica* are distinguished from their congeners by their fine, ashy pubescence; the short-pedicellate, elongate ovaries and fruits; the petals darker than the tube or sepals; and the subtetragonous stigma. The closest relative is *F. pallescens,* which occurs on the opposite side of the Ecuadorian Andes from *F. sylvatica* and which shares the subracemose flowers, darker pet-

als, and elongate ovaries on short pedicels. It differs, however, in its pale whitish floral tube, semisucculent stems, and thin membranous, long petiolate leaves. *Fushia sessilifolia* also has small bicolored flowers with short pedicellate, elongate fruits, but the flowers are borne in panicles, and the leaves are subsessile, lanceolate, and quaternate.

Fuchsia nigricans is the most widespread of the Venezuelan fuchsias and occurs continuously from Lara to Táchira. It is surprisingly absent from most of the Colombian side of the Cordillera Oriental, however. In Colombia, it is only one of two species that occurs in all three cordilleras. With this wide range it is found sympatrically with five species, *F. gehrigeri, F. putumayensis, F. sessilifolia, F. venusta,* and *F. verrucosa*. Hybrids have been found with all of these except *F. verrucosa*; a detailed analysis of the different hybrids is included in the section on interspecific hybridization.

9. Fuchsia sylvatica Bentham, Pl. Hartw. 176. 1845. Munz, Proc. Calif. Acad. Sci. IV. 25:68. 1943, pro parte; Opera Bot., Ser. B, 3:23. 1974, pro parte. TYPE: Ecuador, Prov. Pichincha, woods at Guayán, W slopes of Volcán Pichincha, 1841–1843, *Theodor Hartweg 984* (K Bentham Herb., holotype; photograph, MO; BM, BREM, CGE 2 sheets, G, K Hooker Herb., LE, OXF, isotypes).

Erect to scandent shrubs 1–2.5 m tall. Young growth finely canescent; older stems with tan, fissured bark. Leaves mostly ternate, opposite, or rarely quaternate, membranous, finely reticulate-veined and sometimes rugulose, elliptic to (ob-)ovate, acute to attenuate at the base, mostly acute at the apex, 4–15 cm long, 2–8 cm wide, medium-dark green and strigillose above, pale green to tinged red and strigillose below; secondary veins 11–18 on either side of the midvein; margin remotely gland-denticulate. Petioles strigillose, 6–34 mm long. Stipules dark purple, narrowly triangular, 1–2 mm long, ca. 0.7 mm wide, thick at the base, subulate at the apex, subpersistent. Flowers generally numerous in long, straggly, terminal or subterminal racemes; rachis arching-pendant or sometimes ± twisted, 5–20 cm long; bracts ovate-cordate, subsessile, tightly grouped. Pedicels slender, divergent to pendant, 3–10 mm long. Ovary narrowly cylindric-fusiform, often narrowed towards the apex, 6–10 mm long, 2–3 mm thick. Floral tube narrowly funnelform, 14–22 mm long, 2–3 mm wide and slightly bulbous at the base, gradually widened above until 3.5–7 mm wide at the rim, canescent-strigillose outside, pilose inside in lower ½. Sepals lanceolate, acute, 10–13 mm long, 3–5 mm wide, spreading at anthesis. Tube and sepals red to rose red. Petals darker, crimson, narrowly elliptic-oblong, acute, 5–10 mm long, 2–4 mm wide. Nectary green, shallowly 4-lobed, ca. 1.5 mm high. Filaments red, 5–7 mm and 3–5 mm long; anthers oblong, 1.5–2 mm long, ca. 1 mm thick, dull white. Style glabrous to sparsely pilose, light red; stigma capitate, subtetragonous, 2–3 mm long, 2–4 mm wide, 4-lobed in upper ½, pink, slightly exserted beyond the anthers. Berry subcylindric-fusiform, gradually narrowed towards the apex, ± verrucose before maturity, 13–17 mm long, 5–7 mm thick, red purple to subtranslucent; seeds ca. 1.5 mm long, ca. 0.8 mm wide. Gametic chromosome number $n = 11$.

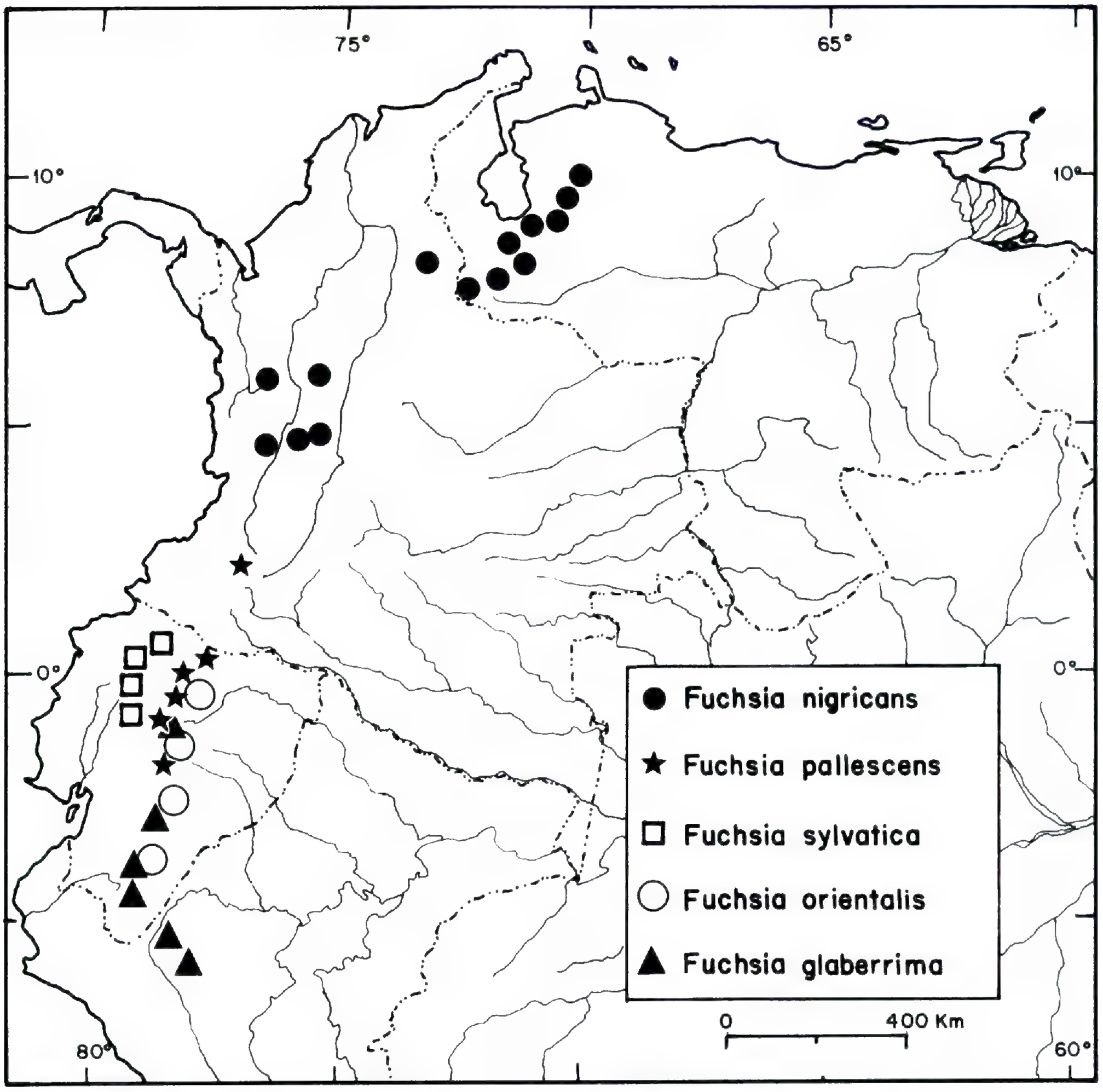


FIGURE 57. Distribution of the *Fuchsia nigricans* species group.

Distribution: Ecuador. Scattered shrubs on the western slopes of the Andes from Cotopaxi to Imbabura Provinces, in mid-elevation cloud forest, growing in moist soil in thickets, along streams, or on roadside banks; 2,600–3,100 m (Fig. 57).

Representative specimens examined: ECUADOR, COTOPAXI: 5 km above Pilaló towards Latacunga, *Berry & Berry 2550* (MO); 4 km E of Pilaló, *Escobar 1095* (MO). IMBABURA: 25 km W of Laguna Cuicocha on road to Intá, *Berry 3171* (MO, QCA). PICHINCHA: Los Alpes, NW side of El Corazón, *Acosta Solis 7074* (F); 26 km from Chillogallo towards Chiriboga, *Berry 2537* (MO, Q); Km 32–33 W of Chillogallo, *Berry & Escobar 3237* (MO), *3238* (MO), *3239* (MO), *3240* (MO); Sigsal, above Chiriboga, *Berry & Escobar 3244* (MO); 11–12 km NW of Nono, *Croat 38823* (MO); W side of Volcán Pichincha, *Jameson 709* (BM, G, K, LE, OXF 2 sheets); valley of Lloa, *Jameson s.n.* (K); Km 32–38 old road Quito to Santo Domingo de los Colorados, *Luteyn & Lebrón-Luteyn 5608* (MO, NY); Alaspongo, trail from Nono to Gualea, *Mexia 7703* (BM, GH, K, MO, NY, POM, S, U, UC, US).

This species is closely related to *F. nigricans*, and their differences, distributions, and relationships are discussed under that species. It occurs sympatri-

cally with *F. macrostigma*, *F. scabriuscula*, and *F. sessilifolia*. No flowering hybrids were found with any of these species, but it is likely that nonflowering hybrids were growing between Nono and Nanegal, where I found a dense thicket of *F. scabriuscula*, *F. sessilifolia*, and *F. sylvatica* growing together in direct contact in 1977. The vegetative similarity of *F. scabriuscula* and *F. sylvatica* makes confirmation of this problematical, however.

On the western slopes of Prov. Carchi along the Colombian border, plants were found that agreed well with *F. sylvatica* in all morphological characters except for their much longer flowers and fruits. Floral tubes are 45–54 mm long and fruits ca. 23 mm long in *Holm-Nielsen et al. 5752* (AAU, S; Ecuador, Prov. Carchi, Km 60 of Tulcán-Maldonado road, 2,700 m) and *Berry 3149* (MO, QCA; 68 km W of Tulcán to Maldonado, 2,500 m). Pollen stainability in these collections is high, 88.8% in *Holm-Nielsen et al. 5752* and 94.2% in *Berry 3149* (500 grains counted). More intensive collections are needed from this and surrounding areas, because it is very rich in intermediate forms and local endemics (see *F. cinerea*, *F. corollata*, *F. dependens*, and *F. polyantha*).

10. Fuchsia pallescens Diels, Notizbl. Bot. Gart. Berlin-Dahlem 14:34. 1938. Munz, Proc. Calif. Acad. Sci. IV. 25:29. 1943; Opera Bot., Ser. B, 3:20. 1974. TYPE: Ecuador, Prov. Tungurahua, E of Patate, woods above Leito, 2,750 m, 8 March 1935, *Arnold Schultze-Rhonhof 1827* (B, holotype, destroyed in World War II). NEOTYPE: Ecuador, Prov. Tungurahua, vicinity of Patate, Hacienda Leito, 2,800 m, 5 Aug. 1939, *Erik Asplund 8073* (S; photograph MO).

Usually well-branched herbs to subshrubs 5–18 dm tall. Branchlets subterete, semisucculent, 2–4 mm thick, subglabrous; older stems 4–8 mm thick, with dull tan, finely fissured bark. Leaves opposite or ternate, thin membranous, elliptic-ovate, attenuate to rounded at the base, subacuminate at the apex, 3.5–7(–9.5) cm long, 1.5–4(–5) cm wide, velvety dark green and glabrous to strigillose above, paler below and subglabrous to puberulent, especially along the veins; secondary veins 5–7(–9) on either side of the midvein, lightly impressed above and subelevated below; margin gland-denticulate. Petioles slender, (15–)25–40(–50) mm long, glabrous to puberulent, green. Stipules triangular, 1–1.5 mm long, ca. 0.5 mm wide, succulent at the base, sometimes connate and reflexed on lower nodes, subpersistent. Flowers few and pendant in upper leaf axils or subracemose at the tips of branches with reduced leaves 10–20 mm long subtending the flowers. Pedicels slender, drooping, 7–15 mm long. Ovary narrowly cylindric, 5–8 mm long, 2–3 mm thick. Floral tube narrowly funnelform, 18–25 mm long, slightly nodose at the base and 1.5–2 mm wide, gradually widened above until 4–5 mm wide at the rim, glabrous to puberulent outside, densely pilose inside in lower ½. Sepals lanceolate, acute to long acuminate, 9–15 mm long, 3–4 mm wide, spreading at anthesis. Tube and sepals subnitid whitish pink to pale red. Petals considerably darker, maroon to dark red, broadly elliptic, acute to rounded at the apex, 5–8 mm long, ca. 4 mm wide, suberect. Nectary unlobed, 1–1.5 mm high. Filaments light pink, 5–7 mm and 3–5 mm long; anthers oblong, 1–1.5 mm long, ca. 0.8 mm wide, cream to pale yellow. Style glabrous, light pink; stigma capitate, 4-lobed in upper ½, 1.5–2.5 mm long, 2–3 mm wide, white. Berry oblong,

narrowed apically, rugose before maturity, turning lustrous purple, ca. 13 mm long, 4–6 mm thick; seeds ca. 1 mm long, 0.6–0.7 mm wide. Gametic chromosome number $n = 11$.

Distribution: Ecuador and southern Colombia. Moist, shady cloud forest habitats, restricted to the eastern slopes of the Andes in Ecuador from Azuay to Napo, and disjunct to the west slopes of the Cordillera Occidental in Cauca, Colombia; 2,550–2,900 m (Fig. 57).

Specimens examined: COLOMBIA, CAUCA: near ridge of Cordillera Occidental, Km 41 of Popayán-Uribe-Munchique road, *Berry 3570* (COL, MO); Mount El Derrumbo, *Killip 7992* (NY, PH, US), *Lehmann 5956* (K). ECUADOR, CHIMBORAZO: road from Pusucucho to El Placer, *Acosta Solis 7255* (F), *7281* (F). IMBABURA: Trail to Río San Pedro, ridge S of Río Clavadero, E of Cayambe, *Wiggins 10444* (DS, NY, POM). NAPO: Km 209 of Quito-Baeza road, below Papallacta, *Berry & Berry 2524* (MO, Q), *2527* (MO, Q); above Cuyuja, *Berry & Escobar 3248* (MO); Salcedo (San Miguel), Km 55 on Salcedo-Napo road, *Boeke 901* (MO); Santa Bárbara de Sucumbios, 10 km E of Santa Bárbara, *Harling 4105* (S); between Cuyuja and Papallacta, *Holm-Nielsen et al. 6815* (AAU, NY, S). TUNGURAHUA: between Leito and La Cima, *Acosta Solis 9025* (F); between La Cima and Río Chico, *Acosta Solis 10242* (F). AZUAY: Quebradas leading into the Río Collay, 3–8 km N of Sevilla de Oro, *Camp 4897* (GH, NY, RSA, US).

This species is allied to *F. nigricans* and *F. sylvatica* in its subracemose inflorescence of short flowers with dark petals and elongate ovaries. The tube and sepals are unusually pale, however, and the plants are generally more delicate, with thin leaves and semisucculent young stems. Small, nearly herbaceous plants of *F. pallescens* are commonly found growing under large *Gunnera* leaves, though larger, woodier plants can sometimes be found in more open areas such as roadbanks. It occurs sympatrically with *F. scabriuscula* and *F. vulcanica*.

Fuchsia pallescens occupies ranges distinct from both *F. nigricans* and *F. sylvatica*. The disjunction from western Colombia to the eastern slopes of Ecuador is similar to that of *F. putumayensis* and is possibly due to a past migration across the Nudo de Pasto.

The limited number of specimens available makes an accurate assessment of the variability of this species difficult, but three variants can be mentioned: 1) *Harling 4105* (S), from northern Napo near the Colombian border. The petioles of this collection are short, and the leaves have 8 or 9 secondary veins instead of the normal 5 or 6. Pollen stainability of this individual is 60% (500 grains). 2) *Camp 4897* (GH, NY, RSA, US), from Azuay. The floral tubes of this collection are short (ca. 18 mm), as are the nonacuminate sepals, and the petals may not be as dark as in other populations. 3) Colombian collections. *Berry 3570* is puberulent and has a few more leaf veins, but otherwise is similar to the main Ecuadorian populations. *Killip 7792* (NY, PH, US) and *Lehmann 5956* (K) have rather stout stems and larger leaves. The tube and sepal color cannot be determined from these specimens, however, so their placement in this species should be considered tentative.

11. **Fuchsia orientalis** P. Berry, **sp. nov.** TYPE: Ecuador, Prov. Napo, between Cosanga and Baeza, trailside in open woods, 2,000 m, 5 May 1935, *Ynes Mexia 7337* (US 1662406, holotype; photograph, MO; K, NA, UC, isotypes).

Fuchsia sylvatica sensu Munz, Opera Bot., Ser. B, 3:23. 1974.

Frutex 1–2 m altus, ramulis foliis junioribus puberulo-strigulosis. Folia opposita, raro ternata, membranacea, anguste elliptica vel obovata, basi acuta, attenuata vel inaequalia, apice acuta vel acuminata, 6–21 cm longa, 2.5–6 cm lata, supra subnitida subglabrataque subtus pallidioria nervis marginibusque plerumque strigulosis vel puberulis; nervis secundaris utroque latere 12–17 subtus plerumque prominentibus, margine integerrima; petiolis strigulosis, 8–20 mm longis; stipulis lanceolatis, subpersistentibus, 1.5–3 mm longis, 0.5–0.8 mm latis, in nodis veternis crassisculis et recurvatis. Flores scarlatini vel aurantiaco-rubri, pauci vel numerosi in racemis abruptis terminalibus vel axillaribus dispositi; rhachidi 5–16 cm longa; bracteis persistentibus lanceolatis 10–25 mm longis, 3–10 mm latis, petiolis 3–5 mm longis; pedicellis 3–7(–12) mm longis; ovario oblongo, 4–5 mm longo. Tubi florales anguste infundibuliformes 15–21 mm longi, basi ca. 2 mm lati et parum bulbosi inde leviter constricti superne gradatim dilatati summo 3.5–5 mm lati, extus strigulosi intus infra medium retrorso-villosi. Sepala oblongo-lanceolata, 6–8 mm longa, 3–4 mm lata. Petala late elliptica, 5–8 mm longa, 3–4 mm lata. Filamenta antisepala 6–7 mm longa, antipetala 4–5 mm longa, antheris late oblongis, ca. 1.5 mm longis, ca. 1 mm latis, albidis. Stylus ruber plerumque glaber, stigmate capitato 1.5–2 mm longo, ca. 2.5 mm lato apice leviter 4-fisso. Bacca cylindrica, verrucosa, 9–12 mm longa, ca. 5 mm crassa, rubro-purpurea; seminibus 1–1.1 mm longis, ca. 0.7 mm latis. Numerus gameticus chromosomatum $n = 11$.

Shrubs 1–2 m tall. Young growth puberulent to strigillose. Leaves opposite, rarely ternate, membranous, narrowly elliptic to obovate, acute to attenuate or unequal at the base, acute to acuminate at the apex, 6–21 cm long, 2.5–6 cm wide, subnitid and subglabrous to strigillose above, paler and mostly strigillose or puberulent along the veins and margin below; secondary veins 12–17 on either side, mostly prominent below, margin entire. Petioles strigillose, 8–20 mm long. Stipules lanceolate, 1.5–3 mm long, 0.5–0.8 mm wide, mostly persistent and becoming thick and recurved on lower nodes. Flowers few to many in abrupt, terminal and axillary, bracteate racemes; rachis 5–16 cm long, elongating in fruit; bracts lanceolate, persistent, 10–25 mm long, 3–10 mm wide, with petioles 3–5 mm long. Pedicels strigose, 3–7(–12) mm long. Ovary cylindrical, 4–5 mm long, 1.5–2 mm thick. Floral tube narrowly funnelform, 15–21 mm long, ca. 2 mm wide and slightly bulbous at the base, gradually widened above until 3.5–5 mm wide at the rim, strigillose outside, retrorse villous in lower ½. Sepals oblong-lanceolate, 6–8 mm long, 3–4 mm wide. Tube and sepals scarlet to orange red. Petals red to orange red, oblong to broadly elliptic, 5–8 mm long, 3–4 mm wide. Nectary unlobed or shallowly lobed, 1–1.5 mm high. Filaments red, 6–7 mm and 4–5 mm long; anthers broadly oblong, ca. 1.5 mm long and ca. 1 mm wide, white. Style red, mostly glabrous; stigma capitate, 1.5–2 mm long, ca. 2.5 mm wide, 4-cleft at the apex. Berry cylindrical, verrucose, 9–12 mm long, ca. 5 mm thick, red purple; seeds 1–1.1 mm long, ca. 0.7 mm wide. Gametic chromosome number $n = 11$.

Distribution: Ecuador. Scattered shrubs in low elevation cloud forest on the eastern slopes of the Andes from Napo to Zamora-Chinchipe, 1,200–2,600 m (Fig. 57).

Specimens examined: ECUADOR, AZUAY: 1–8 km N of Sevilla de Oro, *Camp E-4251* (NY, P, RSA). LOJA: 14 km E of Loja towards Zamora, *Berry & Escobar 3199* (MO, QCA); Km 10.5 of Loja-Zamora road, *Holm-Nielsen et al. 3552* (AAU, S). MORONA-SANTIAGO: between Río Soldo and La Esperanza, road to Huamboya, *Acosta Solis 7343* (F); Cordillera de Cutucú, W slopes, between Logroño and Yaupi, *Madison et al. 3342* (MO); trail between Mirador and Pailas, *Steyermark 54280* (NY). NAPO: Cordillera Guacamayo, slope toward Urcusiqui, *Asplund 9578* (S); Cosanga, 20 km S of Baeza, *Balslev & Madsen 10340* (AAU, MO); 10 km from Baeza to Cosanga, *Berry & Escobar 3246* (MO); Cerro Antisana, E of Borja, *Grubb et al. 1050* (K, NY); Río Cosanga, near Cosanga, *Kirkbride & Chamba*

4012 (MO). TUNGURAHUA: Río Mapoto, *Penland & Summers 282* (F, GH, POM, RSA). ZAMORA-CHINCHIPE: Huaico, SE of Loja, *Espinosa E-660* (RSA); Km 16 Loja to Zamora, *Sparre 16507* (S).

This species typically has elongate racemes with persistent, narrowly lanceolate bracts. This character is also found in the larger leaved *F. pilosa*, but *F. orientalis* is most closely allied to *F. glaberrima*, which has larger flowers and more sessile leaves, but similar thick stipules and persistent bracts. In Napo, it is a low elevation species on slopes leading down into the "Oriente" or Amazon lowlands of Ecuador. It occurs sympatrically there with *E. scabriuscula*. In southern Ecuador, it occurs between 2,000 and 2,600 m, considerably higher than in the north.

12. **Fuchsia glaberrima** I. M. Johnston, Contr. Gray Herb. 75:32. 1925. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):555. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:66, *pl. 10, fig. 55*. 1943; Opera Bot., Ser. B, 3:15. 1974. TYPE: Ecuador, Prov. Tungurahua, valley of Río Pastaza, between Baños and Cashurco, 1,300–1,800 m, 25 Sept. 1923, *Albert S. Hitchcock 21750* (GH, holotype; photograph, MO; NY, US, isotypes; photograph of US isotype, UC).

Simple to few-branched shrubs 1–3 m tall. Branchlets subterete, 3–5 mm thick, glabrous or minutely and sparsely puberulent on youngest growth, green to red-purple. Leaves opposite or subopposite near the branch tips, firmly membranous to subcoriaceous, oblanceolate, obtuse to attenuate at the base, acute to acuminate at the apex, 10–24 cm long, 4–8 cm wide, subnitid and glabrous above, pale to usually flushed red-violet below and glabrous to finely puberulent along the nerves; secondary veins 8–20(–26) on either side of the midvein; margin entire. Petioles short, stout, 3–8 mm long. Stipules triangular, thick, mostly connate and recurved between the lower, opposite leaves, 2–3 mm long, 2–4 mm wide, persistent. Flowers 3–ca. 15 in terminal, bracteate, drooping racemes; rachis 2–4 cm long or occasionally extending 6–12 cm long in fruit; bracts sessile, lanceolate, 10–30 mm long, subtending the alternately disposed flowers. Pedicels 3–12 mm long, mostly glabrous. Ovary oblong, 7–9 mm long, 2–3 mm thick. Floral tube narrowly funnelform, 22–35(–40) mm long, ca. 2 mm wide at the base, slightly constricted above the nectary, then gradually widened above until 6–7 mm wide at the rim, glabrous outside, densely pubescent inside for most of length. Sepals oblong-lanceolate, 8–11 mm long, 4–5 mm wide, shortly acute-tipped, subtetragonous in bud, spreading at anthesis. Tube and sepals red to orange red. Petals red, broadly elliptic-obovate, 7–11 mm long, 5–6 mm wide, rounded at the apex. Nectary unlobed, ca. 1.5 mm high. Filaments red, 5–6 mm and 3–4 mm long; anthers oblong, ca. 2 mm long, ca. 1 mm wide. Style densely pilose or occasionally glabrous; stigma capitate, subtetragonous, ca. 2 mm long, ca. 3 mm wide, 4-lobed apically, shortly exserted beyond the anthers. Berry oblong, ca. 15 mm long, 7–9 mm thick; seeds ca. 2 mm long, ca. 1 mm wide.

Distribution: Scarce shrubs of the lower cloud forest limit from Tungurahua, Ecuador, to Amazonas, Peru, 1,600–1,900 m (Fig. 57).

Specimens examined: ECUADOR, LOJA: W slopes of Cordillera del Cóndor NW of Nudo de Sabanilla, around Tambo Cachiyacu, SE of Yangana, *Steyermark 54786* (NY). MORONA-SANTIAGO: Plan de Milagro, ca. 10 km NW of Indanza, *Jorgensen OHJ-38* (NY); W slopes Cordillera de Cutucú, trail

from Logroño to Yaupi, *Madison et al. 3531* (MO). TUNGURAHUA: upper Río Pastaza, *Spruce 5031* (K). ZAMORA-CHINCHIPE: Río de San Francisco, *Poortman 318* (P). WITHOUT LOCALITY: *Lobb s.n.* (K); *Pearce 329* (K). PERU, AMAZONAS: 12–20 km E of La Peca, Serranía de Bagua, *Barbour 2581* (MO), *2668* (MO), *2686* (MO), *2718* (MO), *2734* (MO), *4171* (MO); *Gentry et al. 23031* (MO), *23023* (MO); Yambrasbamba, *Mathews 803* (OXF); Taulia, *Mathews 1484* (K).

This species can be readily distinguished by its large, opposite, oblanceolate, and subsessile leaves that are usually violet flushed below. It also has unusually thick, persistent stipules. *Fuchsia glaberrima* closely resembles *F. orientalis* in its abrupt racemes, short pedicels, and persistent bracts, but the latter has shorter flowers and longer petiolate leaves. Both are restricted to the low, eastern slopes of the equatorial Andes, but they are not known to occur together or to intergrade.

This is the only species in the section to occur both north and south of the Amotape-Huancabamba zone in southern Ecuador and northern Peru. Plants from the southern end of the range (Amazonas and Loja) have more secondary veins (ca. 20 vs. ca. 10) and less hairy styles than central Ecuadorian collections. Their floral tubes are also somewhat longer (35 mm vs. 25 mm), and the inflorescences are looser and less congested. Both vein number and style pubescence can vary locally, however; *Gentry et al. 23031* (MO) from Amazonas has fewer than 20 veins and a pilose style, but the close-by *Gentry et al. 23023* (MO) has over 25 secondary veins and a glabrous style.

13. **Fuchsia macrophylla** I. M. Johnston, Contr. Gray Herb. 75:35. 1925. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):557. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:66, *pl. 10, fig. 56*. 1943. TYPE: Peru, Dept. Junín, La Merced, Hacienda Schunke, 1,200 m, Aug.–Sept. 1923, *Francis Macbride 5616* (F 536655, holotype; photographs, NY, POM, UC; GH, US, isotypes).

Erect to scandent shrubs 1–3 m tall with spreading branches. Young growth minutely puberulent, branchlets 3–6 mm thick, usually red-purple tinged; older branches with light brown, finely fissured bark. Leaves opposite or less often ternate, firmly membranous, (narrowly) elliptic to lanceolate or (ob-)ovate, acute to cuneate at the base, acute to acuminate at the apex, basal leaves generally considerably larger than the upper ones, 16–27 cm long, 5–9 cm wide, light to dark green and subglabrous above, paler and subglabrous below; secondary veins 14–19 on either side of the midvein, reddish and prominent below, anastomosing into a distinct submarginal vein; margin subentire. Petioles subglabrous, 10–35 mm long, reddish. Stipules dark, lanceolate to triangular, sometimes connate, 1–2 mm long, 0.5–0.8 mm wide, mostly deciduous. Flowers few to numerous in short lateral racemes or on short side branchlets; rachis 2–10(–12) cm long. Pedicels slender, spreading, 10–26(–32) mm long, reddish. Ovary ellipsoid, 4–5 mm long, ca. 2 mm thick. Floral tube narrowly funnelform, 19–25 mm long, ca. 2 mm wide and slightly nodose at the base, gradually widened above until 4–6 mm wide at the rim, puberulent to subglabrous outside, pilose inside for most of length. Sepals lance-oblong, acute, 8–9 mm long, 3–4 mm wide, short-pointed in bud. Tube red, sepals red with green tips. Petals scarlet, elliptic to lanceolate, acute, 7–10 mm long, 3–4 mm wide. Nectary unlobed, ca. 1 mm high. Filaments red, 4–7 mm and 3–4 mm long; anthers oblong, 1.4–1.6 mm long, ca. 0.8 mm wide, dull white. Style pubescent for most of length, red; stigma capitate, ca. 2 mm long and wide,

shallowly 4-lobed, cream to pink, exserted 1–2 mm beyond anthers. Berry subglobose to ellipsoid, 10–13 mm long, 8–9 mm thick, nitid dark purple; seed tan, 1.1–1.3 mm long, ca. 0.7 mm wide. Gametic chromosome number $n = 11$.

Distribution: Central to southern Peru, from Loreto and Huánuco to Puno; in moist thickets in low elevation cloud forest and subtropical wet forest; 1,200–2,000 m (Fig. 56).

Representative specimens examined: PERU, AYACUCHO: 8 km below Jano, road from Tambo to Ayna, *Berry 3053* (MO, USM); between Tambo San Miguel, Ayna, and Hacienda Luisiana, *Dudley 11816* (F, MO, NA 2 sheets, NY, USM); Ccarrapa, between Huanta and Río Apurimac, *Killip & Smith 22353* (F, GH, K, NY, S, US). CUZCO: Tunquimayo, Quince Mil, Prov. Quispicanchis, *Vargas 11776* (CUZ, MO); between Tambomayo and Consuelo, along Río Tambomayo, Prov. Paucartambo, *West 7113* (GH, MO, UC). HUÁNUCO: trail from Puente Durand to Éxito, Pampa Hermosa, *Mexia 8142* (BH, BM, F, G, GH, K, MO, NA, NY, S, U, UC); cuesta San Toribio, quebrada Cutama, *Vargas 5370* (BH, CUZ); Palo Marcado, *Vargas 15336* (MO, USM). JUNÍN: 44 km W of Satipo towards Concepción, *Berry & Aronson 3080* (MO, USM); Cumbre Yacunay above La Merced, *Hutchison 1173* (F, G, GH, MICH, MO, NY, S, UC, US); Pichis trail, *Killip & Smith 25436* (F, GH, NY, US); Pangoa, *Mathews 1169* (K, OXF); Utcuyacu, *Woytkowski 35382* (F, MO 2 sheets, UC, USM). LORETO: La Divisoria, *Ferreyra 1654* (MO, RSA, US 2 sheets, USM); below La Divisoria, *Ferreyra 4299* (MO, US, USM); vicinity of Aguaytía, *Mathias & Taylor 5150* (F, RSA, US, USM). PASCO: San Luis de Oxapampa, *Infantes 1492* (MO, USM); Vitoc, *Isern 2556* (F); road to Pozuzo, *Pearce 213* (K); Pozuzo, *Pearce 541* (K); between La Merced and Oxapampa, *Saunders 547* (BM); Quillasú, *Soukup 3343* (COL); Villa Rica, *Woytkowski 7325* (GH, MO). PUNO: trail between La Oroya and Mina Santo Domingo, *Hodge 6025* (CUZ, GH, US, USM).

This species is closely allied to the only other two species in the section with lateral inflorescences, *F. ovalis* and *F. macropetala*. These inflorescences emerge from leaf axils in the mid-section of the stem and not apically as in most other species (Fig. 40). *Fuchsia ovalis* differs in its heavily pilose pubescence and long petiolate leaves, whereas *F. macropetala* is extremely similar to *F. macrophylla*, differing mainly in its longer flowers and fruits. Both these species grow close by in the Cordillera Azul near the Loreto-Huánuco border, and despite their close similarity, no intermediate forms have been observed.

Fuchsia macrophylla is isolated from other species in the section by its low altitudinal range. It is the lowest elevation species in Peru and enters into the subtropical vegetation zone. Much of this formation has been destroyed on the eastern slopes of the Andes, and this species was probably much more common until the recent increase in habitat destruction.

14. **Fuchsia macropetala** Presl, Rel. Haenk. 2:28. 1831. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):557. 1941. TYPE: Peru, Dept. Huánuco, in mountains of Huánuco, 1790, *Thaddeus Haenke* (PR 495859, holotype; photograph, MO). Although no definite locality information is given, Haenke visited the Cordillera Azul in 1790 (Kühnel, 1960), where he might have collected this specimen.

Erect to scandent shrubs 1.5–3 m tall. Young growth minutely puberulent; older branches glabrescent, with finely-splitting, tan brown bark. Leaves opposite, firmly membranous, elliptic, mostly acute at the base, acute to shortly acuminate at the apex, (7–)9–18 cm long, (3–)4–8 cm wide, subglabrous to strigillose on both surfaces, sometimes purple flushed below; secondary veins 13–18 on either side of the midvein, often reddish, prominent below and anastomosing into

a submarginal vein; margin subentire. Petiole subglabrous, 6–16 mm long. Stipules lanceolate to triangular, sometimes connate, 1–2 mm long, ca. 0.7 mm wide, mostly deciduous. Flowers few to many in lateral racemes or on short side branchlets 1–6(–10) cm long. Pedicels subglabrous, 9–26 mm long, reddish. Ovary ellipsoid, 6–8 mm long, ca. 3 mm thick, light green, finely strigillose and ± verrucose. Floral tube subcylindric, 32–45 mm long, 2.5–3 mm wide at the base, slightly constricted to ca. 2 mm wide above the nectary and gradually widened above until 5–7 mm wide at the rim, finely strigillose outside, pilose inside in lower ½. Sepals lanceolate, 10–13 mm long, 3–5 mm wide, spreading at anthesis. Tube and sepals bright red. Petals red, elliptic-oblong, 10–12 mm long, 4–6 mm wide. Nectary mostly unlobed, 1–1.5 mm high. Filaments red, 7–10 mm and 5–8 mm long; anthers oblong, ca. 2 mm long, ca. 1 mm wide. Style pubescent for most its length, red; stigma capitate, ca. 2 mm long, 2–4 mm wide, slightly 4-cleft apically, dull white to pink, exserted 4–10 mm beyond the anthers. Berry ellipsoid, 15–18 mm long, 7–10 mm thick, dull dark purple; seeds 1.5–2 mm long, dull dark purple; seeds 1.5–2 mm long, 0.9–1.2 mm wide.

Distribution: Central Peru. Known only from the Cordillera Azul, which is a semi-isolated Andean spur to the east of the main Andean cordilleras of Peru and which runs along the Huánuco-Loreto border before joining the main cordillera in southern Huánuco. Clearings and roadsides, 1,600–1,800 m (Fig. 56).

Specimens examined: PERU, HUÁNUCO: 37 km E of Tingo María, near ridge of La Divisoria, *Berry & Aronson 3089* (MO, USM), *3090* (MO, USM), *3090-B* (MO); La Divisoria, *Gentry et al. 18880* (MO); Cuchero, 9°35′S, 75°45′W, *Poeppig 1081* (BM, W), *s.n.* (W 2 sheets); Km 194, La Divisoria, *Ridoutt s.n.* (*Vargas 4654*) (CUZ), *USM 13004* (MO, USM). LORETO: Divisoria, 59 km from Tingo María, *Allard 21226* (RSA, US), *21297* (RSA, US); just E of crest at La Divisoria, *Berry & Aronson 3091* (MO); near Divisoria, *Ferreyra 991* (GH, MO, NY, RSA, US, USM); *2244* (MO, US, USM), *Smith & Vera 364-H-E* (RSA). WITHOUT LOCALITY: *Poeppig 156* (G, LE, P); *Poeppig s.n.* (LE).

This is the only species with lateral inflorescences (Fig. 40) and floral tubes more than 32 mm long. It is closely related to *F. macrophylla*, which shares the same low altitude distribution, lateral inflorescences, and large, elliptic leaves. *Fuchsia macrophylla* has shorter flowers with green sepal tips and smaller, rounder berries, however. These are the only species of *Fuchsia* known from the low Cordillera Azul, but it is not known if the two grow together. Further field study will be required to determine how these closely related species are isolated or if any intermediates occur.

15. Fuchsia ovalis Ruiz & Pavón, Fl. Peruv. Chil. 3:87, *pl. 324, fig. a.* 1802. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):560. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:64, *pl. 10, fig. 54.* 1943. TYPE: Peru, Dept. Huánuco, near Muña, 1778–1788, *Hipólito Ruiz & José Pavón* (MA 11/87, lectotype, here designated; photograph, MO). There are also four other Ruiz and Pavón sheets of this species at MA, two at BM, and one each at F, G, MO, and NY, but these lack label information and may not be part of the same collection set.

Fuchsia polyanthella I. M. Johnston, Contr. Gray Herb. 75:36. 1925. TYPE: Peru, Dept. Huánuco, Muña, trail to Tambo de Vaca, ca. 2,700 m, 5–7 June 1923, *Francis Macbride 4290* (F 535372, holotype; photographs, NY, UC; GH, K, isotypes).

Erect to scandent shrubs 1–3 m tall. Young leaves and shoots mostly densely pilose; older branches pilose to glabrescent, 5–13 mm thick, with light tan, finely fissured bark. Leaves opposite to quaternate, firmly membranous, broadly elliptic to ovate, rounded to acute at the base, acute to short acuminate at the apex, mature leaves 8–16 cm long, 3–7.5 cm wide, dark green and strigose above, paler green and strigose-pilose below, especially along the veins; secondary veins 14–17 on either side of the midvein, emerging from the midvein at ±90° and becoming gradually incurved towards the margin, anastomosing into a submarginal vein; margin subentire to obscurely denticulate. Petioles pilose, 2–7 cm long, reddish. Stipules lanceolate on young nodes, often triangular, connate, and recurved on older stems, 2–4 mm long, 2–3.5 mm wide. Flowers several to numerous in lateral racemes or panicles; rachis 5–10 cm long; bracts narrowly lanceolate, long acuminate, pilose, 6–12 mm long. Pedicels pilose, ± divergent, 10–20 mm long. Ovary cylindrical, 5–7 mm long, ca. 2 mm thick, loosely pilose. Floral tube narrowly funnelform, 18–20 mm long, ca. 2 mm wide and slightly bulbous at the base, gradually widened above until 3–4.5 mm wide at the rim, sparsely pilose outside, densely retrorse villous inside in lower ½. Sepals lanceolate, acuminate, 10–13 mm long, 3–3.5 mm wide, usually noticeably longer than the petals, with tips forming a point ca. 2 mm long in bud. Tube and sepals red. Petals red, oblong, acute, 5–9 mm long, ca. 3 mm wide. Nectary shallowly 4-lobed, ca. 1.2 mm high. Filaments light red, 5--6 mm and 3–4 mm long; anthers oblong, ca. 2 mm long, ca. 1 mm wide. Style glabrous, reddish; stigma capitate, ca. 3 mm long, ca. 2 mm wide, slightly 4-cleft apically, exserted 2–3 mm beyond the anthers. Berry cylindrical or ellipsoid, 12–13 mm long, ca. 6 mm thick, subtetragonous, red purple; seeds 0.9–1.1 mm long, ca. 0.7 mm wide.

Distribution: Central Peru. Restricted to Depts. Huánuco, Pasco, and Junín, rare in cloud forest thickets; 2,000–2,800 m (Fig. 56).

Specimens examined: PERU, HUÁNUCO: Muña, *Lobb 114* (K), *Pearce 511* (K), *Weberbauer 6721* (F); Chinchao, *Ruiz & Pavón s.n.* (BM); Saraypampa, *Woytkowski 34193* (F, UC); Huamincha, *Woytkowski in 1946* (USM). JUNÍN: Chuquishuinca, 2 km above Huacapistana, between Tarma and San Ramón, *Ferreyra 454* (MO, USM); San Juan, near Huacapistana, *Ferreyra 11031* (MO); Vitoc, *Martinet 1585 bis* (P); above Huacapistana, *Sandeman in 1938* (K); WITHOUT LOCALITY: *Lobb s.n.* (K 2 sheets); *Pearce s.n.* (BM).

This species is easily recognized by its large, broad, long-petiolate leaves and densely pilose pubescence on the leaves and flowers. The leaves, bracts, pubescence, and flower size are similar to those of *F. pilosa,* but it is placed with *F. macrophylla* and *F. macropetala* in the same species group because of its lateral inflorescence.

Fuchsia ovalis is rare, and the most recent collection is from 1955 in a now deforested area (the Chanchamayo valley). Because of this, its sympatric occurrence with other species is unknown.

16. Fuchsia pilosa Fielding & Gardner, Sert. Pl. *t. 27.* 1844. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):561. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:65. 1943. TYPE: Peru, Dept. Amazonas, Taulia, S of Molinopampa, 1835–1841, *Andrew Mathews 1492* (OXF, holotype; photograph, MO; BM, CGE, K 2 sheets, isotypes).

Fuchsia asperifolia K. Krause, Repert. Spec. Nov. Regni Veg. 1:169. 1905. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):547. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:65. 1943. TYPE: Peru, Dept. Amazonas, between Tambos Bagazán and Almirante, E of Chachapoyas on path to Moyobamba, 2700 m, 1904–1921, *August Weberbauer 4445* (B, holotype, destroyed in World War II; photograph, F).

Shrub 1–2 m tall with densely hirsute young growth, the hairs usually whitish, shaggy, erect, 1.0–1.6 mm long; older branches glabrescent, with light tan, finely striated bark. Leaves opposite to quaternate, usually ternate, membranous, narrowly to broadly elliptic or oblanceolate, acute to attenuate at the base, acute to acuminate at the apex, 5–16 cm long, 2–7 cm wide, matte green and subglabrous to villous on upper surface, slightly paler and villous below; secondary veins 10–12 on either side of the midvein, sulcate above and prominent below, margin subentire. Petioles hirsute, 12–60 mm long. Stipules ca. 1 mm thick, prominent, lanceolate to triangular, 3–4 mm long, ca. 2 mm wide, often connate and recurved on lower nodes, persistent. Flowers numerous and crowded at the tips of terminal, drooping racemes; rachis 3–20 cm long; bracts narrowly lanceolate, 5–15 mm long. Pedicels slender, 3–5 mm long, ca. 1.5 mm thick. Floral tube narrowly funnelform, 16–20 mm long, slightly bulbous and ca. 2 mm wide at the base, gradually widened above until 4–5 mm wide at the rim, sparsely to moderately hirsute outside, densely retrorse villous inside in lower ½. Sepals lanceolate, long acuminate, 6–8 mm long, 2.5–3 mm wide, with free, divergent tips 2–3 mm long in bud, divergent with recurved tips at anthesis. Tube and sepals bright orange red. Petals orange red, delicate, oblong-elliptic, 6–8 mm long, 3–4 mm wide, recurved at anthesis. Nectary unlobed, ca. 1 mm high. Filaments orange red, 4–5 mm and 2–3 mm long; anthers oblong, 1.5–2 mm long, ca. 1 mm wide, white. Style glabrous, light red; stigma capitate, subtetragonous, 4-cleft apically, 1.5–2 mm long, 2–3 mm wide, dull white, exserted 1–2 mm beyond the anthers. Berry ellipsoid-oblong, 4-sulcate before maturity, 15–19 mm long, 10–12 mm thick, sparsely hirsute, reddish; seeds tan, ca. 1.5 mm long, 0.9–1.0 mm wide. Gametic chromosome number $n = 11$.

Distribution: Northern Peru. Endemic to mid-elevation cloud forest in the mountains E of the Río Utcubamba in Dept. Amazonas; 1,600–2,400 m (Fig. 56).

Specimens examined: PERU, AMAZONAS: 9–11 km E of Molinopampa on Chachapoyas-Mendoza road, *Berry & Escobar 3618* (MO, USM), *3619* (MO, USM), *3620* (MO, USM); above Pomacocha, *Ferreyra 15170* (MO); Tresleras, on Pomacocha-Yambrasbamba trail, *Ferreyra 15233* (MO); Almirante, *Mathews 1481* (K), *Sandeman 54* (K, OXF); mountains S of Tambo de Ventilla, *Pennell 15794* (USM); Mendoza, *Woytkowski 8202* (MO), *8325* (US).

This is one of several species endemic to Dept. Amazonas in northern Peru. It is most easily recognized by its stiff, hirsute pubescence, broad leaves, and terminal, drooping inflorescence of red orange, short-pedicellate flowers. Because of floral and foliar similarities to *F. ovalis*, it is placed in the *F. macrophylla* species group, but in its abrupt, terminal inflorescences and thick, persistent stipules it resembles other species such as *F. wurdackii* and *F. glaberrima*.

Fuchsia pilosa grows together with *F. rivularis* in cloud forest thickets in Dept. Amazonas. No hybrids or intermediates were found between them, which is at least partly due to differences in habit. Although their basal stems may at times be entangled, *F. pilosa* persists as a low, upright shrub with dangling inflo-

rescences, while *F. rivularis* is a scandent-climbing species with long branches and subaxillary flowers that are usually found higher above ground than *F. pilosa*.

17. **Fuchsia putumayensis** Munz, Proc. Calif. Acad. Sci. IV. 25:62, *pl. 8, fig. 52.* 1943. TYPE: Colombia, Com. Putumayo, Mocoa, 23 May 1935, *Hernando García-Barriga 4639* (US 1593482, holotype; photographs, NY, POM, UC; AAU, COL, isotypes).

Shrubs or subshrubs 1–3 m high. Young growth minutely puberulent; branchlets terete, 2–5 mm thick, green to dull purple; older stems pale tan gray, with finely fissured bark. Leaves opposite, firmly membranous, elliptic, rounded to acute at the base, acute to subacuminate at the apex, 6–15 cm long, 3–7 cm wide, matte green and glabrous above, pale green and subglabrous to finely puberulent below along the subelevated nerves; secondary veins 9–13 on either side of the midvein, impressed above; margin subentire. Petioles 6–15 mm long, puberulent to subglabrous. Stipules lance-deltoid, thick at the base and subulate at the apex, occasionally connate, 1–2 mm long, 0.4–0.8 mm wide, deciduous. Flowers numerous in mostly compact, terminal and subterminal racemes; rachis 1–4(–10) cm long; bracts lance-linear, 10–25 mm long, ± recurved, often deciduous. Pedicels slender, divergent, puberulent, 8–25 mm long. Ovary oblong, 4–5 mm long, 1.5–2 mm thick, puberulent, reddish. Floral tube narrowly funnelform, 15–27 mm long, 2–2.5 mm wide at the base, slightly constricted to 1.5–2 mm wide above the nectary, gradually widened above until 4–7 mm wide at the rim, finely puberulent outside, pubescent inside in the lower ⅓. Sepals lanceolate, acuminate, 8–11 mm long, 3–5 mm wide, with a 1.5–2 mm long tip in bud, divergent at anthesis. Tube and sepals nitid orange to coral red. Petals orange red, delicate, elliptic-oblong, 6–9 mm long, 3–4 mm wide, obtuse or mucronate at the apex, somewhat erose-margined, strongly spreading and recurved at anthesis. Nectary unlobed, 1–1.2 mm high, ca. 0.8 mm thick. Filaments orange red, 4–6 mm and 2.5–4 mm long; anthers elliptic-oblong, 1.5–2.3 mm long, ca. 1 mm wide, cream. Style glabrous, light red; stigma subglobose, slightly 4-lobed apically, cream to pink, exserted shortly above the anthers. Berry oblong-ellipsoid, 10–12 mm long, 5–9 mm thick, subnitid red purple; seeds tan, 1–1.2 mm long. 0.6–0.8 mm wide. Gametic chromosome number $n = 11$.

Distribution: Colombia and Ecuador. Low cloud forest shrubs in the Cordillera Occidental of Colombia from Antioquia to Valle, and on the eastern slopes of the Cordillera Central and Cordillera Oriental in Colombia and Ecuador from Cauca south to Napo; 1,400–2,100 m (Fig. 58).

Specimens examined: COLOMBIA, ANTIOQUIA: trail Encarnación-Parque Nacional Las Orquídeas, *Gentry & Rentería 24607* (MO). CAUCA: Río Villalobos, vicinity of Río Sauzita, *Schultes & Villarreal 5156* (COL, GH), *5173* (F, GH). CHOCÓ: 53–55 km W of Ansermanuevo on road to San José del Palmar, *Berry 3561* (COL, MO), *3562* (COL, MO), *3563* (COL, MO); Km 120–135 of Tutunendo-El Carmen road, alto Río Atrato, *Forero et al. 6172* (MO); Quebrada El Sucio, above Carmen de Atrato, *Fosberg & Core 21551* (RSA, US); 11 km E of San José del Palmar, *Luteyn et al. 7328* (COL, MO NY). PUTUMAYO: Planada de Minchoy, between Sachamates and San Francisco de Sibundoy, *Cuatrecasas 11436* (COL, F, US); between Sachamates and San Antonio, *Ewan 16684* (COL, F, POM, US); Km 128 from Pasto to Mocoa, *Plowman & Davis 4406* (COL, PSO). RISARALDA: Pueblo Rico, *von Sneidern 5464* (F, RSA, S, US), *5546* (COL, MICH, RSA, S, US). VALLE: "Tokio," above El Queremal,

Berry 3564 (COL, MO); Quebrada Robada, Alto Bonito, drainage of Río Albán, *Cuatrecasas 22323* (F, RSA, VALLE); Quebrada of Río San Juan, above El Queremal, *Cuatrecasas 23933* (F, RSA); Calima valley, *Hugh-Jones 445* (COL, K, US); *Langlassé 60 bis* (G 2 sheets). ECUADOR, NAPO: Cerro Antisana, forest E of Borja, *Grubb et al. 1083* (K, NY); Borja, *Harling 3871* (NY, S); 16.5 km NNE of Santa Rosa, road Baeza-Lago Agrio, *MacBryde 728* (MO); junction Baeza-Lago Agrio road with Río Azuela, *MacBryde 808* (MO, QCA); 28 km E of Baeza, before Salado, *Plowman et al. 3951* (COL, F, GH, MO, S).

This species is part of a group with *Fuchsia lehmannii*, *F. andrei*, and *F. cuatrecasasii* that have flowers usually tightly grouped in short terminal inflorescences with lanceolate or deciduous bracts and ± divergent pedicels. *Fuchsia putumayensis* has uniformly elliptic, opposite leaves like *F. cuatrecasasii*, but shorter, orange flowers with somewhat erose petals as in *F. lehmannii*.

Like *F. pallescens*, this species is disjunct from the western slopes of the Cordillera Occidental in Colombia to the eastern slopes of the Andes in Ecuador and Colombia. Most Ecuadorian populations have longer racemes (ca. 10 cm long) than most collections from Colombia, but occasional Colombian specimens such as *Langlassé 60 bis* (G), from Valle, also have loose inflorescences.

Although *F. putumayensis* is the lowest elevation fuchsia in the northern Andes and is generally altitudinally separated from other species, a probable hybrid with *F. nigricans* (*Robinson 138*, K) was found and is discussed under that species.

18. Fuchsia lehmannii Munz, Proc. Calif. Acad. Sci. IV. 25:61, *pl. 9, fig. 51.* 1943; Opera Bot., Ser. B, 3:17. 1974. TYPE: Ecuador, Prov. Morona-Santiago, east Andes of Sigsig, 1,600–1,800 m, 1850–1903, *Friedrich C. Lehmann 5498* (F 550994, holotype; photographs, MO, NY, POM, UC; GH, K, US, isotypes).

Scandent to erect shrubs 1–3 m tall, mostly with numerous short lateral branches 5–12 cm long near the tips of the main stems. Leaves 2–4 per node, mostly ternate or quaternate, membranous, narrowly (ob-)lanceolate to narrowly elliptic, acute to acuminate at the base, acuminate at the apex, 4–11(–15) cm long, 1–3.5(–4.2) cm wide, subnitid dark green and glabrous above, pale green and glabrous or pubescent along veins below; secondary veins 8–10(–11) on either side of the midvein, impressed above, margin entire. Petioles 4–12(–20) mm long, subglabrous to strigillose, mostly reddish. Stipules lanceolate, 1.5–2 mm long, 0.4–0.8 mm wide, deciduous. Flowers numerous in compact, terminal and subterminal racemes; rachis 0.5–3 cm long, usually ± strigose; bracts narrowly lanceolate, acuminate, usually reflexed, 5–15 mm long, 1–4 mm wide. Pedicels slender, 8–15 mm long, ± divergent, strigose or glabrous. Ovary oblong, 3–5 mm long, 1.5–2.5 mm wide, subglabrous, mostly wine red. Floral tube narrowly funnelform, 22–35 mm long, 1.5–2.5 mm wide and slightly bulbous at the base, narrowed to 1.2–2 mm wide for the basal ⅓, then dilated to 6–9 mm wide before narrowing slightly towards the rim of the tube, glabrous outside, pilose inside in basal ⅓. Sepals narrowly lanceolate, 10–13 mm long, 2.5–4 mm wide, generally long acuminate, 4-angled in bud with a tip 2–3 mm long, strongly divergent to slightly reflexed at anthesis. Tube and sepals nitid orange to coral red. Petals delicate, orange red, narrowly lance-oblong, 8–11 mm long, 2.5–4 mm wide, acute at the tip, undulate and spreading-reflexed at anthesis. Nectary unlobed, ca. 1 mm high.

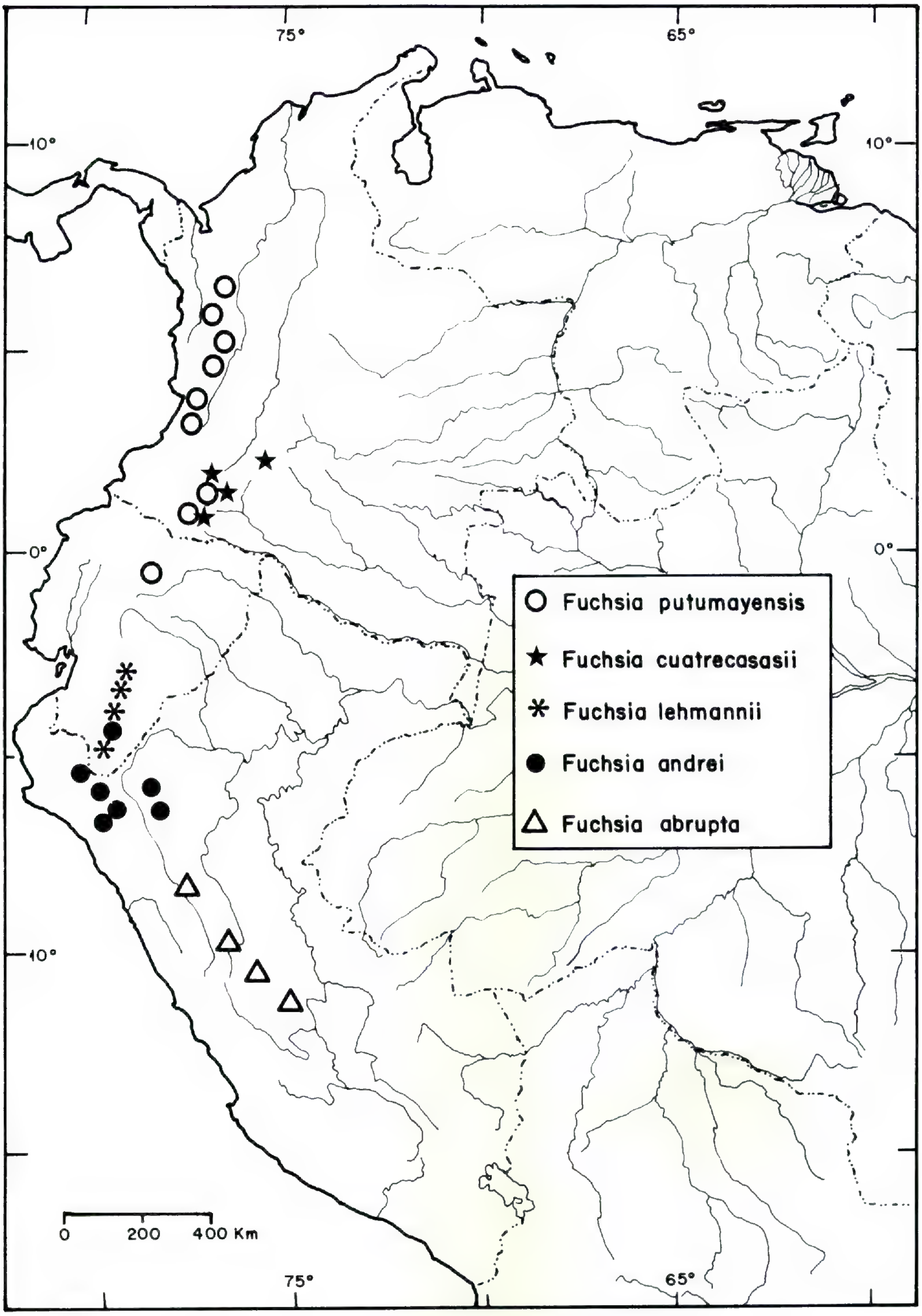


FIGURE 58. Distribution of the *Fuchsia putumayensis* species group.

Filaments orange red, 5–6 mm and 3–4 mm long; anthers oblong, 1.5–2 mm long, 1.1–1.3 mm wide, cream. Style orange red, mostly glabrous or loosely villous in lower ½; stigma capitate, shortly 4-cleft at apex, 2–2.5 mm long, ca. 2 mm wide, dull cream to orange red. Berry oblong-ellipsoid, 11–15 mm long, 7–8 mm thick, turning dark purple at maturity; seeds 0.9–1.1 mm long, 0.7–0.8 mm wide, brown. Gametic chromosome number $n = 11$.

Distribution: Southern Ecuador. Moist thickets, streamsides, and roadbanks on the eastern slopes of Prov. Zamora-Chinchipe and Morona-Santiago; 1,600–2,250 m (Fig. 58).

Representative specimens examined: ECUADOR, MORONA-SANTIAGO: Tambo Chontal to Tambo Consuelo, slopes above Ríos Negro and Chupianza, Seville de Oro trail, *Camp E-1589* (NY, RSA). ZAMORA-CHINCHIPE: 27 km E of Loja to Zamora, *Berry & Escobar 3200* (MO, QCA); Hacienda Montecristi, ca. 40 km NE of Loja, *Espinosa E-1461* (US); Canillones, Río San Francisco, *Fosberg 23165* (COL, NY, RSA, US); 5 km W of Tambo, Loja-Zamora road, *Harling 5865* (NY, S); Km 39 Loja-Zamora road, *Holm-Nielsen et al. 4066* (AAU, COL, MO, NY, S); Km 33 Loja-Zamora road, *Holm-Nielsen et al. 4134* (AAU, COL, MO, NY, S); Río Savonilla, *Lehmann 7858* (F, K, US); below El Retorno, *Mathias & Taylor 5200* (F, RSA, USM); trail from Mirador to Pailas, *Steyermark 54281* (NY); Tambo Valladolid, *Steyermark 54654* (NY).

This species is most closely allied to *F. putumayensis* and *F. andrei,* both species with tight, many-flowered inflorescences of orange red flowers and delicate petals. It has narrower leaves than either of these species, however, longer sepals, and floral tubes that are widest below the rim of the tube. Although it has not been found sympatrically with other fuchsias, its altitudinal and geographical ranges overlap with those of *F. glaberrima* and *F. andrei.*

19. **Fuchsia andrei** I. M. Johnston, Contr. Gray Herb. 75:31. 1925. Munz, Proc. Calif. Acad. Sci. IV. 25:61, *pl. 9, fig. 50.* 1943. TYPE: Ecuador or Peru (locality uncertain), Río de Huarunamaca (as appears on K sheet, transcribed to "Río de Huannamaca" on the sheets at F and NY), 19 Nov. (?) 1876, *Édouard André K.820* (F 537131, holotype; photographs, MO, NY, POM, UC; K, NY, isotypes). I have been unable to find the above locality in maps or gazeteers of either Colombia, Ecuador, or Peru, where André collected in 1876. According to Johnston's protologue, the locality is from Colombia. A detailed list of André's itinerary, however, does not mention this river for either Colombia or Ecuador (Smith, 1965). The last part of André's itinerary in southern Ecuador and northern Peru was not included in Smith's list, however, and that is when André hired H. Poortman to collect for him (L. B. Smith, pers. comm.). Since André had already returned to Europe in Sept. 1876, this collection must have been made by Poortman, who collected mostly in Prov. Loja of southern Ecuador.

Fuchsia osgoodii J. F. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):559. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:60, *pl. 9, fig. 49.* 1943. TYPE: Peru, Dept. Libertad, Uchco, 15 June 1912, *Wilfred H. Osgood & Mary P. Anderson 47* (F 346773, holotype; photographs, NY, UC).

Fuchsia ovalis var. *aberrans* J. F. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):560. 1941. TYPE: Peru, Dept. Cajamarca, Prov. Cutervo, Arenales, S of San Tomás, 3,000 m, 12 Dec. 1938, *Harvey E. Stork & Ovid. B. Horton 10155* (F 1052360, holotype; photograph, NY; G, NA, UC, isotypes).

Shrubs 1–4 m tall. Branchlets terete, 3–8 mm thick, sparsely puberulent to strigillose; older stems 8–14 mm thick, with tan, finely striated bark. Leaves

opposite or less often ternate, membranous, (narrowly) elliptic to obovate, acute to cuneate at the base, subacuminate at the apex, (5–)7–17 cm long, 2–9(–11) cm wide, glabrous above, subglabrous to strigose below on midvein and along margin; secondary veins (8–)12–15 on either side of the midvein; margin entire or subdenticulate. Petioles 6–20(–30) mm long. Stipules triangular, dark, 1.5–2 mm long, ca. 1.5 mm wide, subpersistent. Flowers numerous in short, terminal and subterminal racemes; rachis 2–6 cm long; bracts lanceolate, 6–10 mm long, 2–4 mm wide. Pedicels slender, mostly strigose, ± divergent, (7–)10–18(–25) mm long. Ovary oblong, 5–6 mm long, 2–2.5 mm thick. Floral tube narrowly funnelform, 23–38(–45) mm long, 1.5–2 mm wide and subnodose at the base, narrowed to 1–1.5 mm in basal ⅓, gradually widened above until 4–7 mm wide at the rim, glabrous outside, pilose inside in lower ½. Sepals lanceolate, acute to subacuminate, (6–)8–13 mm long, 4–5 mm wide. Tube and sepals orange to coral red. Petals orange red, oblong, obtuse to acute at the apex, 7–12 mm long, 2.5–4 mm wide, nectary unlobed, ca. 1 mm high. Filaments light red, 6–8 mm and 4–6 mm long; anthers oblong, 1.5–2 mm long, 1–1.2 mm wide. Style light red, glabrous to pilose in lower ½; stigma capitate, 4-cleft apically, 2–2.5 mm long, ca. 2.5 mm wide. Berry oblong-ellipsoid, 10–12 mm long, 6–8 mm thick, green to red; seeds tan, 1–1.2 mm long, 0.7–0.8 mm wide. Gametic chromosome number $n = 11$.

Distribution: Southern Ecuador and northern Peru. Cloud forest and semi-open moist scrub in Prov. Piura, Cajamarca, and Amazonas, Peru and in Prov. Zamora-Chinchipe, Ecuador (1,130–)1,800–3,000 m (Fig. 58).

Specimens examined: ECUADOR, ZAMORA-CHINCHIPE: Tambo de Savanilla, *André K.818* (F, GH, NY). PERU, AMAZONAS: Cordillera Colán SE of La Peca, *Barbour 3995* (MO), *4083* (MO); 13 km E of Molinopampa on Chachapoyas-Mendoza road, *Berry & Escobar 3621* (MO, USM); Km 42 of Carretera Marginal from Pedro Ruiz to Rioja, *Berry & Escobar 3628* (MO, USM); Prov. Bongará, *Ferreyra 15170* (MO 2 sheets), *15233* (MO); E side Cerros Calla-Calla, 5 km above Leimebamba, *Hutchison & Wright 4884* (UC); Río Almirante, *Sandeman in 1938* (K); Mendoza, *Woytkowski 8325* (US); 2–4 km WSW of Pomacocha, Prov. Bongará, *Wurdack 850* (US). CAJAMARCA: above Tabaconas, 18 km SE of Huancabamba, Prov. Jaen, *Fosberg 27835* (MO); Hacienda Taulis, vicinity of the Casa Hacienda, Prov. Hualgayoc, *Hutchison & Bismark 6326* (F, MICH, MO, NY, P, RSA, UC, US); San Andrés, Prov. Cutervo, *López & Sagástegui 5436* (MO, US), *Sagástegui in 1969* (NY), *Velarde Núñez 6971* (Z); Monte Seco, Prov. Hualgayoc, *Soukup 3848* (F, US). PIURA: Cancahaque, *Stork 11428* (UC).

It is difficult to adequately circumscribe this species because the specimens available are from widely scattered localities throughout northern Peru and because it is not possible to determine the type locality. When more critical collections and field observations have been made in this area, the material treated below will probably be found to comprise several distinct taxa. They are grouped together here, however, because of their similar, compact racemes and generally short-tubed flowers with slender pedicels. In these characters, the specimens included under *F. andrei* are related to *F. lehmannii* and *F. putumayensis*. The type specimen and *Hutchison & Bismark 6326* are characterized by their large leaves ca. 16 cm long and ca. 10 cm wide. This and the somewhat narrower floral tubes distinguish them from *F. lehmannii* of southern Ecuador. There are a number of collections from other areas, though, that show the following differences:

Collections from Prov. Cutervo in Dept. Cajamarca. López & Sagástegui 5436, Velarde Núñez 6971, and *Sagástegui s.n.* have small, narrow leaves and floral tubes less than 25 mm long. *Stork & Horton 10155,* though, which Macbride

described as *F. ovalis* var. *aberrans*, has some larger, basal leaves that approach those of the type of *F. andrei*.

Stork 11428. This collection from Cajamarca has floral tubes 42–45 mm long and is recorded as growing at 1,130 m, which is much lower than the other specimens considered here. The area where it was collected has been severely altered, however, and no further populations were found when I visited the area in 1979.

Fosberg 27835. The leaves of this collection are narrowly elliptic as in *F. lehmannii*. The same is true for *Osgood & Anderson 47*, the type of *F. osgoodii*, but it has not been possible to identify the locality of this collection, believed by Macbride to be in Dept. Libertad.

Collections from Dept. Amazonas. These are considerably isolated from the specimens to the west of the Río Marañon, and they occur in wetter, cloud forest habitats. *Wurdack 850* and *Hutchison & Wright 4884* have short tubes just over 20 mm long and small, elliptic leaves with subdentate margins. *Woytkowski 8325* has broad leaves ca. 7 cm wide but similarly short flowers. *Ferreyra 15233* has floral tubes 45 mm long. These wide differences suggest that several different entities might be involved in these collections, but further material is needed to determine their limits.

20. Fuchsia cuatrecasasii Munz, Proc. Calif. Acad. Sci. IV. 25:51, *pl. 7, fig. 40*. 1943; non Munz, Opera Bot., Ser. B, 3:14. 1974. TYPE: Colombia, Com. Caquetá, Cordillera Oriental, E slopes, Quebrada del Río Hacha, open woods in Cajón de Pulido, 1,700 m, 26 March 1940, *José Cuatrecasas 8738* (US 1796401, holotype; photographs, MO, NY, POM, UC; COL, isotype).

Subshrubs 0.5–1.5 m high. Branchlets terete to slightly flattened, 2–6 mm thick, subglabrous, green to reddish purple; older branches with light tan-gray bark. Leaves opposite, elliptic, firmly membranous, acute at both ends, smooth and glossy above, subglossy and finely strigillose below on veins and margins; secondary veins 8–12 on either side of the midvein, ± impressed above, at times purple tinged below; margin subentire. Petioles stout, sparsely strigose, 4–14(–17) mm long, red purple. Stipules triangular, firm, dark purple, 1–2 mm long, ca. 1.5 mm wide, subpersistent. Flowers few to many in a compact, terminal, drooping raceme; rachis 1–5(–8) cm long; bracts lanceolate, 8–18 mm long, reflexed. Pedicels 7–13 mm long. Ovary oblong, 4–7 mm long, 1.5–2.5 mm thick, strigillose, subnitid red purple. Floral tube narrowly funnelform, (28–)35–50(–55) mm long, slightly nodose and 2–3.5 mm wide at the base, narrowed to 1.5–3 mm wide in lower ⅓ and widened above until 6–8 mm wide at the rim, puberulent outside, pubescent inside in lower ⅓. Sepals lanceolate, acuminate, (8–)10–20 mm long, 4–6 mm wide, tips usually free in bud for 2–4 mm. Tube and sepals nitid red to orange red. Petals orange red, elliptic to oblanceolate, 9–15 mm long, 4–6 mm wide, acute at the apex, spreading at anthesis. Nectary unlobed, ca. 1.5 mm high. Filaments orange red, 5–9 mm and 4–5 mm long; anthers oblong, 2–3 mm long, 1–1.5 mm wide. Style sparsely villous in lower ½, orange red; stigma capitate, tetragonous, 4-lobed in upper ½, 2–3 mm long, 2–3 mm wide, cream, exserted 1–4 mm beyond the anthers. Berry ellipsoid, 15–20 mm long, 10–15 mm thick, lustrous red purple; seeds 1.1–1.3 mm long, 0.6–0.8 mm wide.

Distribution: Colombia. Infrequent, low shrubs in moist, open thickets in cloud forest on eastern slopes of the Andes from Caquetá south to Putumayo, 1,400–2,200 m (Fig. 58).

Specimens examined: COLOMBIA, CAUCA: Río Villalobos, between the junction of the Ríos Villalobos and Cauchos, *Schultes & Villarreal 5203* (COL, DS, F, GH, MO, UC, US). HUILA: Km 31 of Pitalito-Mocoa road, *Berry 3594* (COL, MO); Km 28–32 of Pitalito-Mocoa road, near divide, *Luteyn et al. 7538* (COL, MO, NY). PUTUMAYO: Mirador, between San Francisco and Mocoa, *Bristol 542* (COL, DS); between El Silencio and La Cabaña, road from Sibundoy to Urcusique, *Cuatrecasas 11495* (COL, US); Cordillera del Portachuelo, road Sibundoy-Mocoa, *Garcia-Barriga et al. 18635* (COL); El Mirador, San Francisco-Mocoa, *Idrobo & Ospina 2364* (COL); Km 90–91 between Sibundoy and Mocoa, *Luteyn et al. 5043* (COL, MO, NY); San Francisco to Mocoa, *Mora 3440* (PSO), *4460* (COL), *Schultes & Cabrera 18625* (RSA); Km 112 from Pasto to Mocoa, *Plowman & Davis 4348* (COL, PSO); Punto Buenos Aires, Cerro Portachuelo, *Soejarto 1125* (GH, PSO).

The short, terminal racemes of tightly packed flowers in *F. cuatrecasasii* is of the same type found in *F. putumayensis, F. lehmannii,* and *F. andrei.* Its flowers are considerably longer than these species, however, and the leaves are uniformly elliptic, opposite, glossy, firm, and short-petiolate. Vegetatively, *F. putumayensis* is the most closely related species. *Fuchsia cuatrecasasii* occurs sympatrically with *F. putumayensis, F. scabriuscula, F. sessilifolia,* and *F. verrucosa,* but it is rare, and no apparent hybrids have been detected.

21. Fuchsia abrupta I. M. Johnston, Contr. Gray Herb. 75:37. 1925. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):545. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:50, *pl. 7, fig. 39.* 1943; non Opera Bot., Ser. B, 3:10. 1974. TYPE: Peru, Dept. Pasco, along river at Cushi, ca. 1,500 m, 19–23 June 1923, *Francis Macbride 4541* (F 535618, holotype; photographs, NY, POM, UC; GH, K, US, isotypes). Fig. 20.

Fuchsia aspiazui J. F. Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4):547. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:43, *pl. 6, fig. 31.* 1943. TYPE: Peru, Dept. Libertad, Prov. Pataz, valley of the Río Mixiollo, Aug. 1914, *August Weberbauer 7042* (F 629319, holotype; photographs, NY, UC; F 2 sheets, GH, US, isotypes).

Scandent to erect shrubs 1–3 m tall. Young branches semisucculent, terete, 3–6 mm thick, subglabrous to densely hispid; older stems 8–15 mm thick, light tan with finely fissured bark. Leaves opposite or ternate, firmly membranous, narrowly to broadly elliptic or (ob-)ovate, acute at the base, acute to acuminate at the apex, 7–14(–19) cm long, 3–6(–10) cm wide, subnitid dark green and sparsely strigose to subglabrous above, pale and strigose to densely villous or hispid below, especially along the veins; secondary veins 15–22 on either side of the midvein, strongly impressed above, anastomosing into a distinct submarginal vein; margin subentire to obscurely denticulate. Petioles strigose, 4–10 mm long. Stipules conspicuous, dark, (narrowly) triangular, sharply acute-tipped, 3–6 mm long, 2–3 mm wide, often connate, persistent. Flowers few to numerous and usually verticillately disposed in terminal, arching racemes; rachis (8–)10–35 cm long, elongating in fruit; bracts lanceolate, divergent, 15–45 mm long. Pedicels spreading at anthesis and 10–15 mm long, divergent and ascending in fruit, when 15–35 mm long, light red. Ovary cylindric, 7–9 mm long, ca. 2 mm thick, lustrous light red, the ovary or floral tube usually somewhat deflexed so that the distal portion of the flower is pendant. Floral tube narrowly funnelform, 35–50(–60) mm

long, 2.5–3.5 mm wide and bulbous at the base, constricted to ca. 2 mm wide for the basal 5–8 mm of the tube, gradually widened above until 6–10 mm wide at the rim, glabrous outside, densely pilose inside in basal ⅓. Sepals lanceolate, 13–20 mm long, 4–7 mm wide, mostly long acuminate at the apex, cuspidate and tetragonous in transection in bud, conspicuously wider than the rim of the tube, divergent at anthesis. Tube and sepals nitid, bright orange red. Petals orange red, delicate, oblong, round to acute at the apex, 13–19 mm long, 5–7 mm wide, spreading to divergent at anthesis with the apical portion recurved and the margins undulate. Nectary green, shallowly 4-lobed, 2.5–3 mm high and ca. 0.7 mm thick. Filaments orange red, 8–10 mm and 6–7 mm long; anthers oblong, 2.5–3 mm long, ca. 1.5 mm wide, white. Style pale red, glabrous; stigma capitate, 2–3 mm long, 2–3 mm wide, 4-cleft apically, pale red. Berry cylindrical-ellipsoid, 18–22 mm long, ca. 10 mm thick, purplish; seeds tan, 1.1–1.4 mm long, 0.8–1.0 mm wide. Gametic chromosome number $n = 11$.

Distribution: Central Peru. Scattered shrubs in cloud forest thickets on the eastern slopes of the Andes from Depts. Libertad to Junín, 1,500–2,700 m (Fig. 58).

Representative specimens examined: PERU, HUÁNUCO: Carpish, *Ferreyra 1719* (MO, RSA, US, USM); Carpish, above Acomayo, *Hutchison et al. 5920* (F, NY, RSA, UC, USM); above Chinchao towards summit of Carpish, *Mathias & Taylor 4033* (F, RSA, USM); Tumanga, *Woytkowski 7951* (US). JUNÍN: 57–58 km above Satipo on road to Concepción, *Berry & Aronson 3077* (MO, USM), *3078* (MO); Km 175 Satipo-Concepción, *Seibert 2379* (MO, POM, US). PASCO: Pozuzo, *Pearce 537* (K).

Fuchsia abrupta is distinguished by its noticeably veiny leaves (due to the numerous, impressed secondary veins), large, persistent stipules, and long, terminal inflorescences with divergent to ascending pedicels and cylindrical fruits. Its affinities are unclear, but despite its elongate racemes, it is placed in the *F. putumayensis* species group because of its divergent pedicels, orange flowers with delicate petals, and narrowly lanceolate bracts. In dried specimens, it may be confused with *F. corymbiflora,* but that species has finely puberulent leaves, rounder fruits, and shorter racemes and pedicels.

The specimen described as *F. aspiazui* has non-apiculate buds and unusually large leaves, but it has the same characteristic inflorescence and vegetative traits of *F. abrupta*. *Sandeman 4503* (K; Peru, Dept. Junín above Huacapistana, ca. 2,000 m, Oct. 1943) is like *F. abrupta* in all characters except its much shorter floral tubes (17 mm long). *Sandeman 4585* (K, OXF) from the same locality, is morphologically intermediate and is probably a hybrid with *F. decussata*. It is discussed further under that species. *Fuchsia abrupta* also occurs sympatrically with *F. ceracea, F. corymbiflora, F. denticulata,* and *F. ferreyrae*.

22. Fuchsia petiolaris Humboldt, Bonpland & Kunth, Nov. Gen. Pl. 6:104. 1823. Munz, Proc. Calif. Acad. Sci. IV. 25:34. 1943. *Fuchsia petiolaris* var. *typica* Munz, Proc. Calif. Acad. Sci. IV. 25:35, *pl. 4, fig. 21*. 1943. Based on *F. petiolaris* HBK. TYPE: Colombia, Dept. Cundinamarca, near Bogotá, ca. 2,500 m, July–Sept. 1801, *Alexander von Humboldt & Aimé Bonpland* (P, holotype, not seen; photograph, F; microfiche, MO).

Fuchsia quinduensis Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 6:105. 1823. TYPE: Colombia, Dept. Tolima or Quindío, in the Quindío Andes, ca. 2,500 m, Sept.–Dec. 1801, *Alexander von Humboldt & Aimé Bonpland* (P, holotype, not seen; photograph, F; microfiche, MO).

Fuchsia curviflora Bentham, Pl. Hartw. 177. 1845. TYPE: Colombia, Dept. Cundinamarca, in Andes near Bogotá, ca. 3,000 m, 1841–1843, *Theodor Hartweg* (K, holotype).

Fuchsia smithii Munz, Proc. Calif. Acad. Sci. IV. 25:36, *pl. 4, fig. 21.* 1943. TYPE: Colombia, Dept. Santander, vicinity of Vetas, 3,200–3,250 m, 16–20 Jan. 1927, *Ellsworth Killip & Albert C. Smith 17300* (GH, holotype; photograph, UC; A, F, NY, US, isotypes).

Fuchsia petiolaris var. *bolivarensis* Munz, Proc. Calif. Acad. Sci. IV. 25:35, *pl. 4, fig. 22.* 1943. TYPE: Colombia, Dept. Antioquia ("Bolivar" on Pennell's label), below Páramo de Cháquiro, Cordillera Occidental, 2,800–3,100 m, 24 Feb. 1918, *Francis W. Pennell 4324* (NY, holotype; photographs, GH, POM, UC). The leaves of this collection are quite slender, but are within the range of those of *F. petiolaris*.

Low shrubs 0.5–2 m tall or climbing-scandent in trees to 5 m above ground. Young growth puberulent to pilulose; branchlets terete, 1.5–3 mm thick, puberulent to ferrugineous-pilose, green to light red purple; older branches 5–12 mm thick, with reddish tan, exfoliating bark. Leaves mostly ternate, up to 6 per whorl, firmly membranous to subcoriaceous, narrowly lanceolate to elliptic or obovate, acute to narrowly cuneate at the base, mostly acute at the apex, (1.5–)3–9(–11) cm long, (0.5–)1–3(–4.5) cm wide, medium to dark matte green and glabrous to puberulent above, pale green and subglabrous to puberulent or pilose below; secondary veins (4–)6–10(–11) on either side of the midvein; margin denticulate to serrulate or rarely subentire. Petioles (2–)5–20 mm long. Stipules lance-linear, 2–3 mm long, ca. 0.5 mm wide, subpersistent. Flowers few to many, axillary. Pedicels pendant, (10–)15–40(–55) mm long. Ovary ovoid, 5–8 mm long, 2–2.5 mm thick. Floral tube narrowly funnelform until the slightly constricted apex, (30–)35–50(–62) mm long, 2.5–4(–6) mm wide and somewhat bulbous at the base, narrowed to 1.5–3(–5) mm wide in the lower ⅓ of the tube, then gradually to rather abruptly widened until (5–)6–11(–12) mm wide at the rim, strigillose to puberulent outside, pilose inside for most of length. Sepals ovate-lanceolate, conspicuously flared outwards from the tube at the base and 1–3 mm wider in bud than the rim of the tube, acute to acuminate, 11–23 mm long, (4–)6–8(–9) mm wide, with coherent or spreading tips in bud and the lobes sometimes splitting open in the middle before anthesis, spreading-divergent at anthesis, at times the basal ½ divergent and the upper ½ erect. Tube dull to subnitid rose pink, sepals usually paler, sometimes with greenish tips. Petals bright red pink, narrowly lanceolate to lance-elliptic, (narrowly) acute to rarely obtuse at the apex, (8–)12–16(–20) mm long, (4–)5–7(–8) mm wide, generally unguiculate at the base, margin smooth to occasionally serrulate, mostly with finely pubescent hairs over the dorsal surface or longer villous hairs along the midvein, rarely (sub-)glabrous, suberect at anthesis. Nectary green, unlobed or 4-lobed, 2–4 mm high. Filaments pink, 8–15 mm and 5–12 mm long; anthers oblong, 2.5–3 mm long, 1.5–2 mm wide, dull white. Style densely pilose in basal ½–¾, pink; stigma globose, 4-lobed at apex, 2–3 mm long, 2–4 mm wide, cream to pink, exserted 5–15 mm beyond the anthers. Berry globose to ellipsoid, 8–18 mm long, 7–13 mm thick, dark red at maturity; seeds tan, 2–3 mm long, 1–1.5 mm wide. Gametic chromosome number $n = 11$.

Distribution: Colombia and Venezuela. Low shrubs or lianas in thickets of high elevation cloud forest or in páramo shrub islands; in the Cordillera Oriental from Huila to Norte de Santander and just into Venezuela in southern Táchira; in the Cordillera Central from northern Valle to Antioquia; and in the Cordillera Occidental in Antioquia; (2,400–)2,900–3,900 m (Fig. 59).

Representative specimens examined: VENEZUELA, TÁCHIRA: between Fátima and San Vicente de la Revancha, *Fernández 1981* (MY); headwaters of the Río Quinimarí, above "Las Copas" below the Páramo de Judio, 18–20 km S of San Vicente de la Revancha, *Steyermark et al. 100795* (VEN). COLOMBIA, ANTIOQUIA: Páramo Frontino, near Llano Grande, *Boeke 250* (MO); summit of Morro Pelado, Anocosca-Abriaquí road, *Core 456* (RSA, US); Páramo de Sonsón, *Guarín 3470* (COL, US). BOYACÁ: Quebrada de San Paulino, near Alto Ritacuva, Sierra Nevada del Cocuy, *Barclay & Juajibioy 7279* (RSA); Páramos NW of Belén, headwaters of Quebrada Minas, *Cleef 1854* (U); between Soatá and Cocuy, Valle de la Uvita, El Hatico, *Cuatrecasas & García-Barriga 1161* (COL, F, US); between Soatá and Cocuy, Páramo del alto de Cañultal, *Cuatrecasas & García-Barriga 1183* (COL, F, US); Quebrada de Susacón, *Cuatrecasas & García-Barriga 9815* (COL, POM, US); above Guicán, Sierra Nevada de Cocuy, *Grubb et al. 70* (COL, K, MSC, US); near Laguna Seca, Sierra Nevada de Cocuy, *Grubb et al. 602* (COL, K, MSC, US); Ramiriquí, towards Laguna Negra, *Huertas & Camargo 6324* (COL); near Montalbán, road Duitama-Charalá, *Langenheim 3470* (COL, UC, US); Laguna la Colorada, Páramo de Pisba, *Rangel et al. 525* (COL); La Rusia, NW of Duitama, *Uribe-Uribe 1075* (COL, US). CALDAS: Páramo de Las Letras, *Barclay & Juajibioy 6293* (COL, MO, RSA); SW slopes of Nevado de Ruiz, Termales, *Cuatrecasas 9218* (COL, F, US); Páramo de Ruiz, *Lehmann 3067* (BM, K, US); 35 km NE of Manizales, *Madison 1335* (GH); San Félix, *Tomás 1866* (BH). CUNDINAMARCA: Subachoque to Cerro El Tablazo, *Berry 3539* (COL, MO); below Páramo de Choachí, *Berry 3542* (COL, MO); ridge between Fómeque and Laguna de Chingaza, Cuatro Vientos, *Cuatrecasas & Idrobo 26973* (US); Páramo de Chingaza, around Laguna Grande, *Cuatrecasas & Idrobo 26992* (US); Río San Juan, above San Juan, *Fosberg 20797* (RSA, US); Páramo de Sumapaz, Río Arroz, *Fosberg 20835* (US); near Bogotá, *Hartweg 990* (BM 2 sheets, BREM, CGE, K, OXF); Guadalupe, Bogotá, *Haught 5061* (POM, US), *5621* (COL, POM, US); Monserrate, Río de San Francisco, near Bogotá, *Hawkes & García-Barriga 69* (BM, COL, K, RSA, US); Páramo de Cruz Verde, near Bogotá, *Pennell 2056* (NY); Río San Cristobal, near Bogotá, *Pennell 2379* (GH, MO, NY, US); Boquerón de Chipaque, *Schneider 621a* (COL); Montserrate, *Triana 198* (K, P, US); La Calera, Páramo de Palacio, *Uribe-Uribe 6886* (COL); 20 km SE of Gigante, *Little 8686* (US). META: Río Arroz, well above confluence of Quebrada Pedregal, *Fosberg 20916* (US). NORTE DE SANTANDER: 7 km above Pamplona to Bucaramanga, *Berry 3533* (MO); Chitagá, near Presidente, *Cuatrecasas & García-Barriga 10053* (COL, F); Pamplona, *Funck & Schlim 1646* (BM, CGE, F, G, LE, OXF, P, W); 20 km S of Abrego, Las Jurisdicciones, Cerro de Oroque, border with Dept. Cesar, *García-Barriga & Jaramillo 19758* (COL), *19808* (COL); around Ocaña, *Kalbreyer 426* (K); between Mutiscua and Pamplona, *Killip & Smith 19734* (A, GH, NY, US); W slopes Páramo del Hatico, Toledo to Pamplona, *Killip & Smith 20714* (GH, NY, US); Pica-pica valley, above Tapatá, N of Toledo, *Killip & Smith 21121* (GH, NY). QUINDÍO: Alaska, above Salento, *Pennell 9381* (PH); Páramo del Quindío, *Pennell & Hazen 10058* (NY, PH). RISARALDA: Campoalegre-San Ramón ridge, E of Santa Rosa de Cabal, *St. John 20850* (COL, NY, RSA, US). SANTANDER: Páramo de la Cruces, *Funck & Schlim 1307* (BM, G, LE, P, W); La Baja, *Funck & Schlim 1305* (BM, G 2 sheets, LE, OXF, W); edge of Páramo Las Vegas, *Killip & Smith 15734* (A, F, NY, US); between California and Las Vegas, *Killip & Smith 17236* (A, GH, NY, US); vicinity of Vetas, *Killip & Smith 17335* (A, GH, US), *17361* (A, GH, NY, US), *17386* (A, GH, NY, US); W slopes of Páramo Rico, *Killip & Smith 17755* (A, F, GH, NY, US), *17771* (A, GH, NY, US); Páramo de las Puentes, above La Baja, *Killip & Smith 18211* (A, GH, NY, US); Páramo de Romeral, *Killip & Smith 18577* (A, GH, NY, US). TOLIMA: 47–48 km W of Fresno to Manizales, *Berry 3558* (COL, MO), *3559* (COL, MO); SE slopes Mt. Tolima, Las Mesetas, *Cuatrecasas 2615* (MA 2 sheets); Quindío-La Linea, *Dryander 1939* (US); Volcancitos, *Holton 896* (G, GH, K, NY, UC); along divide near Quindío highway, *Killip & Varela 34600* (BM, COL, POM, US); Quindío, *Humboldt & Bonpland s.n.* (P); Rosalito, near Páramo de Ruiz, *Pennell 3121* (F, GH, MO, NY, US). VALLE: Páramo de Bavaya, Barragán, drainage of Río Bugalagrande, *Cuatrecasas 20042* (F, US, VALLE); Quebrada de Las Vegas páramo, headwaters of Río Tulua, *Cuatrecasas 20249* (F, VALLE).

This is one of the polymorphic, long-tubed, axillary-flowered species of the *Fuchsia petiolaris* species group that are found at high altitudes in the northern Andes. Its main distinguishing characteristics are the slightly constricted floral tubes at the rim (in most cases), the typically ovate-lanceolate sepals that flare out conspicuously at the base from the rim of the floral tube, and the acute, elliptic to lanceolate petals that are usually puberulent or villous on the dorsal surface. The petals are always smaller than the sepals and in some populations are less than half as long. Its closest relative is probably *F. corollata*, which occurs south of the range of *F. petiolaris* in the Cordillera Central. A list of their

TABLE 10. Distinguishing characters of *Fuchsia petiolaris* and *F. corollata*.

	F. petiolaris	*F. corollata*
Leaf texture (when dry)	Smooth	Slightly bullate
Leaf surface (when dry)	Matte	Glossy
Length of glandular teeth on margin	0.1–0.3 mm	0.3–0.5 mm
Floral tube constricted at rim	Usually	No
Floral tube pubescence	Puberulent	Strigose
Petal shape	Lanceolate-elliptic	Rhombic-broadly elliptic
Petal apex	Acute	Obtuse to cuneate
Petal pubescence (dorsal side)	Puberulent to villous, rarely glabrous	Glabrous
Style pubescence	Densely pilose in basal ½–¾	Glabrous to occasionally pilose

distinguishing characters is given in Table 10. The possible affinities of *F. petiolaris* outside of its species group are with *F. gehrigeri,* which commonly has pubescent petals, and similarly large seeds and globose fruits.

Characters that vary widely in *F. petiolaris* are leaf size and shape, floral dimensions, pubescence type on stems and petals, and the size and shape of the berries. Most of the size differences can be attributed to ecological factors. Short petiolate, small-leaved and short-flowered plants typically are found in high, exposed habitats or in trees near open páramo. Well shaded plants in lower, more protected sites are usually more robust, with longer pedicels, and larger leaves and flowers.

Geographical patterns of variation exist in characters such as pubescence and leaf shape, but individuals typical of one area can always be found in the other areas as well. In view of this wide degree of local and regional polymorphism, any attempt to subdivide this group taxonomically seems unwarranted. Some of the patterns of variation are described in the following paragraphs.

Most collections from the northern part of the Cordillera Oriental of Colombia (Boyacá to Norte de Santander) and just over the border into Táchira, Venezuela have short pilose, ferrugineous stem pubescence. Such plants were treated by Munz as *Fuchsia smithii,* and these also differ from most populations from Cundinamarca and the Cordillera Central in their larger, narrower, more reticulate-veined leaves, petals villous mostly along the midvein, and larger, more cylindrical fruits. Variation within this area can also be considerable, however. *Grubb et al. 602* (COL, K, US) has floral tubes 52 mm long but only 5 mm wide; *Cuatrecasas & García-Barriga 10053* (COL, F) has the largest flowers in the species, with tubes 62 mm long and 11 mm wide. Its leaves are broad and nearly entire, unlike most collections from this area.

Some plants of the type described above reach south to Cundinamarca, such as *Cuatrecasas & Idrobo 26973* (US). Plants from the Bogotá area are especially variable, however, but for the most part have fine, canescent vegetative pubescence and round fruits. The degree of petal pubescence is exceedingly variable between populations around Bogotá, with some puberulent over the entire adaxial surface, as in *Hawkes & García-Barriga 69* (BM, COL, K, RSA, US), and others that are entirely glabrous, as in *Haught 5621* (COL, POM, US). The type spec-

imens of *F. petiolaris* and *F. curviflora* are both from the vicinity of Bogotá. The slight curvature of the tubes in *F. curviflora* is not unusual, and though the sepals of the dried specimen are pale, they are by no means white as the description states.

Fuchsia petiolaris is widespread in the Nevado de Ruiz Massif of the Cordillera Central, following the same distribution pattern as *F. venusta*, *F. hirtella*, and *F. nigricans*, all of which are present in both the Cordillera Oriental and the Cordillera Central. Many individuals with small leaves and flowers are found in this area; these plants are often found in trees or in exposed páramo shrub islands where stunting is a common response to the harsh climatic conditions. *Fuchsia quinduensis* was apparently described from one such stunted plant, and *Sandeman 5672* (K, OXF) is a particularly good example of leaf reduction in an exposed plant. Sometimes large, petiolate leaves can be found on the basal portions of specimens that have nearly sessile, tightly grouped small leaves on the upper branches. Sepals on plants from the Cordillera Central are usually more flared at the base than ones from the Cordillera Oriental, and they sometimes split open in bud in the middle before the tips become separated. Petals are puberulent over the entire surface and are mostly narrowly lanceolate and much smaller than the sepals. The fruits are generally small and globose as in most Cundinamarca collections, but the flowers are usually puberulent, and the stems are sometimes ferrugineous as in many Santander collections.

Fuchsia petiolaris has also reached the high northern peaks of the Cordillera Occidental in Antioquia. Although *Boeke 256* (MO), from Páramo Frontino, has long, slender flowers (51–55 mm long, 6–8 mm wide), other characters such as petal shape and pubescence are well within the range of *F. petiolaris*.

Since *Fuchsia petiolaris* is the highest altitude species in its range, it usually occurs alone, but in the Cordillera Central it is occasionally sympatric with *F. hirtella* and *F. hartwegii*. It would be of considerable interest to examine more populations of the Cordillera Central between Valle and Cauca, to see if transitional populations occur between the closely related *F. petiolaris* and *F. corollata*.

23. Fuchsia corollata Bentham, Pl. Hartw. 179. 1845. TYPE: Colombia, Dept. Cauca, near Popayán in woods of Puracé, ascent to Páramo de Guanacas, ca. 3,000 m, 1842, *Theodor Hartweg 993* (K Bentham Herb., holotype; photograph, MO; BM, BREM, CGE 2 sheets, F, G, K Hooker Herb., LE, OXF, P, W 2 sheets, isotypes).

Fuchsia canescens sensu Munz, Proc. Calif. Acad. Sci. IV. 25:26. 1943; Opera Bot., Ser. B, 3:12. 1974.

Fuchsia colombiana Munz, Caldasia 4:109, 110, *fig.* 1946. TYPE: Colombia, Dept. Cauca, Cordillera Central, W slopes, headwaters of Río Palo, páramos between la Quebrada del Duende and Las Casitas, 3,500–3,600 m, 3 Dec. 1944, *José Cuatrecasas 18959* (A, holotype; COL, isotype).

Erect to scandent shrubs 0.5–5 m tall with ascending to divergent branches. Branchlets terete, 2–3 mm thick, strigose, generally red purple; older stems 5–12 mm thick with red tan, exfoliating bark. Leaves ternate or less often quaternate, firmly membranous to subcoriaceous, elliptic to oblanceolate, acute to narrowly cuneate at the base, acute to obtuse at the apex, 20–70 mm long, 7–30 mm

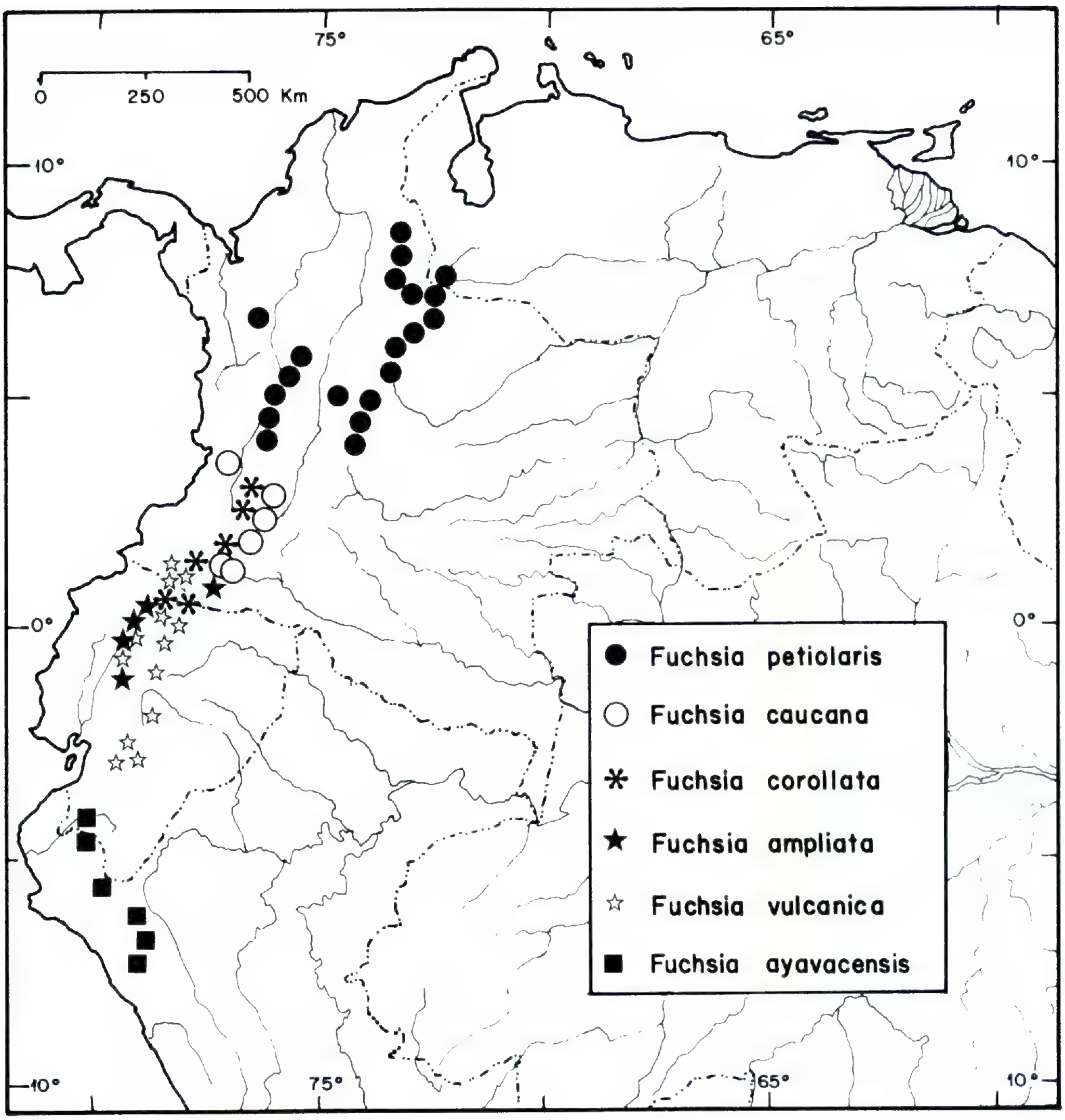


FIGURE 59. Distribution of the *Fuchsia petiolaris* species group.

wide, dark glossy green and glabrous to strigose above, pale green and usually strigose or villous below; secondary veins 3–8 on either side of the midvein, often red below; margin gland-serrulate, the teeth usually conspicuous and mostly 0.3–0.5 mm long. Petioles strigose, 3–12(–22) mm long. Stipules lance-linear, dark, 2–4 mm long, 0.7–1 mm wide, persistent and usually divergent. Flowers axillary and pendant, usually fewer than 6 per branch. Pedicels 12–24 mm long. Ovary ovoid-ellipsoid, 6–7 mm long, 2–2.5 mm thick, subglabrous to strigose. Floral tubes narrowly funnelform, (28–)35–55(–60) mm long, 2.5–3 mm wide and bulbous at base, then narrowed to 1.5–2 mm and gradually widened above until 5–8 mm wide at rim, subglabrous to strigose outside, villous inside in lower ½. Sepals lanceolate to ovate-lanceolate, subacuminate at apex, 10–17(–22) mm long, 5–6(–8) mm wide, sometimes split open in middle in bud, spreading to divergent at an-

thesis. Tube subnitid red pink to scarlet; sepals paler, often greenish towards tips. Petals scarlet, almost always longer than sepals, (broadly) elliptic to rhombic, obtuse to cuneate at apex, attenuate to unguiculate at base, 10–18(–24) mm long, (5–)6–10 mm wide, glabrous to rarely pilose on dorsal nerve, (strongly) spreading at anthesis. Nectary unlobed or shallowly 4-lobed, 1.5–2 mm high, sometimes with a few erect hairs. Filaments red pink, 10–18 mm and 7–15 mm long; anthers oblong to subreniform, 2–3 mm long, 1.5–2.2 mm wide, cream. Style red, glabrous or occasionally pilose; stigma globose, slightly 4-cleft at apex, 2–3 mm long, 2–4 mm wide, cream to light red. Berry subglobose, 9–13 mm long, 8–10 mm thick, purple at maturity; seeds tan, 2–2.6(–3) mm long, (1.0–)1.2–1.6(–2) mm wide. Gametic chromosome number $n = 11, 22$.

Distribution: Southern Colombia and northern Ecuador; high elevation cloud forest and subpáramo shrubs from the Cordillera Central of Colombia in Cauca south to Imbabura, Ecuador, 2,800–3,800 m (Fig. 59).

Representative specimens: COLOMBIA, CAUCA: Pilimbalá, N slopes Volcán Puracé, *Aguirre 311* (COL); 11 km E of Totoró to Inzá, *Berry 3575* (COL, MO); 4 km W of Gabriel López, road Totoró-Inzá, *Berry 3576* (COL, MO); 17 km E of Puracé, *Berry 3582* (MO); headwaters of Río Palo, Quebrada del Duende, *Cuatrecasas 18931* (BH, F, GH, VALLE); Finca Las Mercedes, near Silvia, *Granger & Rodríguez 17* (RSA, US); Manchai, NE of Silvia, *Haught 5122* (COL, POM, US); Páramo Las Delicias, *Lehmann B.T.1058* (GH, K, NY); Paletará, *Pennell 7004* (GH, PH); Páramo de Buena Vista, Huila group, *Pittier 1188* (US). NARIÑO: between Pasto and Túquerres, *André 3182* (K); "El Páramo," Km 15 of Pasto-Ipiales road, *Berry 3146* (MO); Páramo El Tábano, road Pasto-Laguna La Cocha, *Berry 3249* (MO, PSO); 18 km above Pasto, road to Tangua, *Ewan 15918* (BM, DS, POM, US); Laguna La Cocha, *Ewan 16381* (POM, US); road Túquerres-Ipiales, *García-Barriga & Hawkes 13073* (COL, US); road Ipiales-La Victoria, Páramo de la Cortadera, *García-Barriga & Hawkes 13091A* (COL); Volcán de Sotará, *Lehmann 6196* (K); trail from Sapuyes to Páramo de Gualaratán, *Mora 2901* (PSO); Pasto, base of Volcán Galeras, above Obonuco, *Schultes & Villarreal 8023* (COL, RSA, US); Tangua, Cubiján trail, *Uribe-Uribe 5302* (COL, PSO, US). ECUADOR, CARCHI: Tulcán-El Carmelo road, 7 km E of Panamerican Highway, *Berry 3158* (MO), *3159* (MO); between El Carmelo and Santa Bárbara, *Berry 3165* (MO); road Tulcán-El Pun (= El Carmelo), *Mexia 7584* (BH, K, RSA, UC, US). IMBABURA: Hacienda Curubí, 10 km W of Otavalo towards Mojanda, *Berry 3173* (MO, QCA); 11 km W of Otavalo to Laguna de Mojanda, *Berry 3175* (MO, QCA); Mojanda, ca. 10 km SSW of Otavalo, *Sparre 13523* (S).

Probable hybrids between *Fuchsia corollata* and *F. caucana*: COLOMBIA, CAUCA: Páramo de Las Papas, near Laguna Cusiyaco, *Barclay & Juajibioy 5936* (COL, RSA); Volcán de Puracé, *Barkley et al. 18ca.112* (US); 45 km from Popayán on road to Volcán Puracé, *Barkley & Mullen 38C712* (COL, GH); 23–35 km E of Puracé, road to La Plata, *Berry 3583* (COL), *3584* (MO), *3585* (COL, MO); Páramo de Puracé, S of Volcán Puracé along divide, San Francisco, *Cuatrecasas 14644* (BH, F, VALLE); Páramo de Juntas, Km 53 (extension of Páramo de Guanacas), *Cuatrecasas & Willard 26375* (COL); W side of Páramo de Puracé, *Killip & Lehmann 38602* (BH, US); Páramo de Las Papas, between El Boquerón and La Hoyola, *Idrobo et al. 3935* (COL); road Popayán to Puracé, Parque Nacional Puracé, *Lozano & Ruiz 1518* (COL); Parque Nacional Puracé, *Plowman et al. 5335* (COL), *von Sneidern 1843* (S), *1847* (S), *1848* (S), *Uribe-Uribe 3845* (COL, MO). HUILA: 35–40 km E of Puracé on road to La Plata, *Berry 3586* (COL, MO), *3588* (COL, MO).

This is one of several closely allied and polymorphic species in the *Fuchsia petiolaris* species group from high elevations in the Colombian and Ecuadorian Andes. Its most characteristic features are the elliptic-rhombic petals usually exceeding the size of the sepals and the glossy, firm, gland-denticulate leaves that often dry with a slightly bullate texture. Its closest relative is *F. petiolaris*, which occurs in the Cordillera Oriental and Cordillera Central just north of the range of *F. corollata*. Since these species are widespread and variable, clear recognition of the species limits between them can be difficult, especially if one is dealing

only with herbarium specimens. Furthermore, we do not yet know if the two species intergrade in southern Valle Dept. or northern Cauca, where their ranges are in close proximity. Based on the existing specimens, Table 10 presents a summary of characters that can be used to distinguish *F. corollata* from *F. petiolaris*. It must be noted, however, that hybrids of *F. corollata* with other fuchsias are apparently widespread in southern Colombia, and these individuals would generally fall outside the limits designated for the above species.

Munz (1943, 1974) mistakenly synonymized this species under *Fuchsia canescens* because of an erroneously numbered Hartweg collection from Geneva that he examined. *Hartweg 992* is the type number of *F. canescens*, but the specimen at G does not correspond to the holotype at K. It is rather a duplicate of *Hartweg 993*, the type collection of *F. corollata*. Munz was not able to examine the holotypes or other isotypes of these species, so he concluded that *F. corollata* was a synonym of *F. canescens*. The latter species is now known with certainty to be distinct and much rarer than *F. corollata*; it is found mostly on the eastern slopes of the Cordillera Central in southern Colombia and has thick-tubed, orange, canescent flowers and larger leaves than *F. corollata*.

Morphologically similar populations of *F. corollata* are found from Cauca, Colombia to Imbabura, Ecuador. The species may even reach as far south as Pichincha, but the single collection there, *Benoist 4547* (P; west side of Volcán Pichincha), has rather narrow flowers and pilose styles for this species. Different ploidy levels have been found in different parts of the range of *F. corollata*, however. Two collections from nearby populations in Cauca were diploid, and three counts from two distinct populations in Ecuador were tetraploid (Table 4). The only differences noted between these groups were that the tetraploid populations had slightly larger seeds, more markedly rhombic petals with a narrow base, and a common pyramidal shaped growth habit, with sharply ascending branchlets. Their pollen also has variable proportions of triporate grains. Most of these morphological characters vary within the tetraploid populations, however, and some of the Imbabura individuals even have petals that are shorter than the sepals.

Two collections from the western slopes of the Cordillera Occidental in Carchi, Ecuador, *Holm-Nielsen et al. 5580* (AAU, S) and *5674* (S; both from Km 53 of Tulcán-Maldonado road, 3,150–3,250 m), have certain characters of *F. corollata* such as somewhat rhombic petals and green sepal tips in bud, but they have nearly entire, quaternate, membranous leaves that are not typical of this species. More cytological examination and population sampling from southern Colombia (Cauca and Nariño) would help to establish the pattern of ploidy level in *F. corollata* and to detect if any further morphological differences can be correlated with either diploid or tetraploid populations.

A substantial number of specimens from Cauca differ from typical *F. corollata* populations in one or more of the following characters: small, lanceolate leaves 15–30 mm long, few (2–4) secondary veins, entire or subentire leaf margins, petals shorter than the sepals, long floral tubes mostly 55–70 mm long, and the presence of triporate pollen grains. These collections, which are listed separately at the end of the specimens citation list, are believed to be hybrids between *F. corollata* and *F. caucana*. A series of these probable hybrids was examined in

June 1979 along the road from Popayán to La Plata, in Cauca and Huila Depts., on the north face of Volcán Puracé. Ascending from Popayán from the west, *F. corollata* (*Berry 3582*; COL, MO) was collected with *F. canescens* at 3,235 m. *Berry 3583* to *3586* (COL, MO) were collected farther east, at higher elevations in semi-open subpáramo habitats near the divide of the Cordillera Central. Each number of this series comes from a different population along a stretch of several km, where extreme variability in leaf shape and floral dimensions was found. Starting to descend to the east, the first plant recognized as *F. caucana* (*Berry 3587*; COL, MO) was found at ca. 3,100 m growing next to one of the variable forms typical of the upper, intermediate area (*Berry 3588*; COL, MO). Between 10% and 20% of the pollen in the suspected hybrids, *Berry 3583*, *3584*, *3586*, and *3588*, have triporate grains, and stainability varies from 20% in *Berry 3583* to 80% in *Berry 3584*. Triporate grains in *Fuchsia* are sometimes indicators of polyploidy, and gametic and somatic counts of *Berry 3584* indeed proved to be tetraploid. The two counts of *F. corollata* from Cauca and the one count of *F. caucana* from Nariño are all diploid, however, and both *Berry 3582* (*F. corollata*) and *Berry 3588* (*F. caucana*) have entirely biporate and highly stainable (>95%) pollen grains. It is possible, then, that if all the variable collections along the exposed ridge of the Páramo de Puracé are tetraploids, they originated as allotetraploid hybrids of *F. corollata* and *F. caucana*. This is only hypothetical, but could be analyzed experimentally. Additional evidence of hybrid origin for the above series is available from *Berry 3584*. Normal pairing of 22 bivalents was found in meiotic preparations, but the only ripe fruit found on the plant had 35 aborted seeds and 13 ripe ones. These seeds were germinated along with other collections at the University of California Botanical Gardens at Berkeley in 1980, but only one small, weak seedling developed, from which the tetraploid root tip count was made.

Another area where collections variable in leaf texture and petal size occur is the Páramo de Las Papas area of the Macizo Colombiano in southern Cauca. Hybridization may be the cause of this variability as well. The type of *F. colombiana*, *Cuatrecasas 18959* (A), from northern Cauca, is distinguished by its extremely reduced leaves less than 2 cm long, but this may be due at least in part to the high elevation (3,500–3,600 m) where it was collected. Its leaves are not very different from individuals such as *Berry 3585*, from the probable hybrid series discussed above.

Fuchsia corollata is found in close proximity to *F. caucana* in Nariño, and it occurs sympatrically with *F. canescens*, *F. dependens*, and *F. sessilifolia*.

24. Fuchsia caucana P. Berry, **sp. nov.** TYPE: Colombia, Dept. Cauca, 31 km E of Totoró on road to Inzá, E slopes of Cordillera Central, 3,240 m, 8 June 1979, *Paul E. Berry 3577* (COL 107163, holotype; MO 2 sheets, isotypes). Fig. 26.

Fuchsia petiolaris sensu Munz, Proc. Calif. Acad. Sci. IV. 25:34. 1943, pro parte.

Frutex (0.3–)0.5–2 m altus plerumque pauciramosus. Ramuli teretes, subglabrati vel strigosi vel puberuli, albo-virides vel rubro-purpurei; caulibus glabrescentibus cortice subnitida purpureo-brunnea. Folia plerumque ternata interdum opposita raro quaterna, firme membranacea, (anguste) elliptica vel lanceolato-ovata, basi acuta vel rotundata, apice plerumque acuminata, (2.5–)3.5–7(–10) cm longa, (1–)1.5–3.2(–4) cm lata, supra obscure atroviridia, subglabrata sparsim vel strigulosa, subtus pallide

albo-viridia vel strigosa nervis secundariis utroque latere (3–)5–6(–7) subtus saepe rubris, parallelinervis; margine conspicue glanduloso-serrulata, raro subintegerrima; petiolis saepe rubro-purpureis, 2–13(–14) mm longis; stipulis anguste lanceolatis vel linearibus, fuscatis, 3–4 mm longis, 0.5–1 mm latis, subpersistentibus. Flores roseo-cerasinii vel (pallide) purpureo-lavandulacei, pauci in axillis supernis ramorum dispositi; pedicellis dependentibus, 12–28 mm longis; ovario ovoideo-ellipsoideo, glabro vel puberulenti-strigoso, 5–6 mm longo. Tubi florales anguste infundibuliformes, 32–45(–54) mm longi, basi 2–4 mm lati parum bulbosi, plerumque constricti ⅓ parte inferiore inde saepe ± abrupte dilatati, summo 4–11 mm lati, extus glabrati vel puberulenti, intus pilosi. Sepala lanceolata (sub)acuminata (12–)14–17(–22) mm longa, 5–6 mm lata, alabastro apice interdum albido-viridi. Petala plerumque valde breviora quam sepalis, atrorubra vel purpurea, elliptico-ovata, 9–11(–14) mm longa, 5–6(–9) mm lata, obtusa vel cuneata apice interdum mucronulata. Filamenta rosea, antisepala 8–10 mm longa, antipetala 5–7 mm longa; antheris oblongis 3–4 mm longis, 2–3 mm latis luteo-eburneis. Stylus usque ad summum tubi floralis dense pilosus, roseo-ruber; stigmate roseo, late capitato, tetragono, 2–3 mm long, 3.5–4 mm lato, apice leviter 4-fisso. Bacca ante maturitatem 4-sulcata, glabrata vel puberulento-strigosa, in maturitate subglobosa, 11–13 mm longa, 7–9 mm crassa, nitida rubro-purpurea; seminibus rubro-brunneis vel vivide rubris, 2–2.5 mm longis, 1.1–1.8 mm latis. Numerus gameticus chromosomatum $n = 11$.

Usually few-branched shrubs (0.3–)0.5–2 m tall. Branchlets terete, 2–5 mm thick, subglabrous to strigose or puberulent, white green to red purple; older stems with subnitid, purple brown bark. Leaves mostly ternate, occasionally opposite or quaternate, firmly membranous, (narrowly) elliptic to lance-ovate, acute to rounded at the base, mostly acuminate at the apex, (2.5–)3.5–7(–10) cm long, (1–)1.5–3.2(–4) cm wide, dark velvety green and subglabrous to sparsely strigose above, pale whitish green to deep flushed purple and strigose below; secondary veins (3–)5–6(–7) on either side of the midvein, subparallel and ascending towards the tip at ca. 45° to the midvein; margins serrulate with conspicuous glandular teeth, rarely subentire. Petioles glabrous to strigose, usually red purple, 2–13(–14) mm long. Stipules narrowly lanceolate to linear, 3–4 mm long, 0.5–1 mm wide, subpersistent. Flowers few in upper leaf axils. Pedicels pendant, 12–28 mm long. Ovary ovoid-ellipsoid, glabrous to puberulent or strigose, 5–6 mm long, 2.5–3 mm thick. Floral tube narrowly funnelform, occasionally dilated in the middle and constricted again near the rim, 32–45(–54) mm long, 2–4 mm wide and slightly bulbous at the base, usually narrowed to 1.5–3 mm in lower ⅓, then widened to 4–11 mm wide at the rim, glabrous to strigose or puberulent outside, pilose inside for most or the entire length. Sepals lanceolate, (sub-)acuminate at the apex, (12–)14–17(–22) mm long, 5–6 mm wide, with a short point 1–2 mm long in bud, spreading at anthesis. Tube and sepals pink cerise to (light) purple lavender, young buds sometimes whitish green. Petals usually considerably darker than the sepals, (dark) red-purple, elliptic-ovate, 9–11(–14) mm long, 5–6(–9) mm wide, obtuse to cuneate or sometimes mucronate at the apex, suberect at anthesis. Nectary unlobed, ca. 2 mm high. Filaments pink, 8–10 mm and 5–7 mm long; anthers oblong, 3–4 mm long, 2–3 mm wide, yellow cream. Style densely pilose from base to near the rim, red pink; stigma broadly capitate, tetragonous, slightly 4-cleft apically, 2–3 mm long, 3–4 mm wide, pink, exserted 7–16 mm beyond the anthers. Berry 4-sulcate before maturity, glabrous to strigose or puberulent, subglobose at maturity, 11–13 mm long, 7–9 mm thick, lustrous red purple; seeds reddish brown to bright red, 2–2.5 mm long, 1.1–1.8 mm wide. Gametic chromosome number $n = 11$.

Distribution: Southern Colombia. Low shrubs in open thickets in high elevation elfin cloud forest, eastern slopes of the Cordillera Central in Cauca, Huila,

Nariño, and Putumayo, and in the Cordillera Occidental in the Farallones de Cali, Valle, 2,700–3,600 m (Fig. 59).

Representative specimens examined: COLOMBIA, CAUCA: near Río Grande, between San Andrés and Alto Todos los Santos, *Core 1060* (RSA); between Jardín and San Rafael, Quebrada del Río San Marcos, *Cuatrecasas 14711* (F); Alto del Buey, *Escobar & Escobar 1143* (MO); Páramo de Guanacas, *Lehmann 5616* (K); Parque Nacional Puracé, Paletará, *Luteyn & Lebrón-Luteyn 6948* (NY); Puracé, Moscopán, *Yepes-Agredo 274* (COL). HUILA: between Leticia and Parque Nacional Puracé, 63 km SW of La Plata, *Aguirre 274* (COL); 37–40 km E of Puracé, road to La Plata, *Berry 3587* (COL, MO), *3590* (COL, MO). NARIÑO: Páramo de Quilinsayaco, between El Encano and Santiago, *Barclay & Juajibioy 9470* (RSA); above El Encano, Laguna La Cocha, *Balls B7504* (BM, K, NA, UC, US); 24 km E of Pasto on road to Mocoa, *Berry 3252* (MO, PSO); Páramo de Bordoncillo, *Espinal 1023* (COL, PSO); 34 km E of Pasto, Páramo de Quilinsayaco, *Espinosa E3089* (NY); above Laguna La Cocha, 16 km ESE of Pasto, *Fosberg 20445* (RSA, US); El Tábano, *García-Barriga 4560* (COL, US); Buesaco, *García-Barriga et al. 13016* (COL, US); Laguna La Cocha, Ciudadela, near Páramo de Bordoncillo, *Schultes & Villarreal 7575* (COL, GH, K, NY, RSA, US). PUTUMAYO: between Santiago and Laguna La Cocha, *Alston 8398* (BM, COL, K, RSA); 8 km N of Sibundoy, *Bristol 823* (DS, PSO); La Cabaña, headwaters of Río Sibundoy, valley of Sibundoy, *Cuatrecasas 11598* (COL, F, US); Páramo de Bordoncillo, *Cuatrecasas 11709* (COL, US): Páramo El Capuchino, between El Encano and Sibundoy, *García-Barriga et al. 18581* (COL); Páramo de San Antonio, between Laguna La Cocha and Sibundoy, *Schultes 3225* (DS, GH, NY); between La María and Páramo de San Antonio, road from Sibundoy to Pasto, *Schultes & Villarreal 7827* (GH, RSA).

Fuchsia caucana is allied to other long-tubed, axillary-flowered, high-elevation species such as *F. corollata* and *F. petiolaris*. Munz included the specimens he saw of this species under *F. petiolaris*, but *F. caucana* is clearly distinct from that species both morphologically and geographically. Part of this confusion is due to the loss of key characters upon drying, making it difficult to distinguish this species when just herbarium specimens are available. *Fuchsia caucana* can generally be distinguished, though, by its acuminate-tipped leaves with few secondary veins that ascend toward the tip at a sharp (±45°) angle from the midvein. When fresh, the leaves are mostly a matte, velvety green above and much paler or often purple-flushed below. This contrasts with the glossy, dark foliage of *F. corollata*. The floral tubes are different shades of lavender or pink purple, unlike the redder flowers of *F. petiolaris* and *F. corollata*. The petals are often a deep purple and are always darker and considerably shorter than the sepals. In *F. corollata*, the petals usually exceed the sepals and are scarlet colored.

Some variation in tube shape and pubescence occurs between different populations. In Huila and Cauca, most plants are glabrous or strigose with floral tubes that are usually somewhat constricted at the rim. Plants from Nariño and Putumayo are commonly puberulent with narrowly funnelform tubes widest at the rim. The disjunct populations from the Cordillera Occidental in Valle are well within the variation present in the Cordillera Central.

Fuchsia caucana is sympatric with *F. canescens* on the upper, eastern slopes of the Cordillera Central in Cauca and Nariño. Probable hybrids are found around the type locality on the road from Totoró to Inzá and are discussed under *F. canescens*. Extensive intergradation between *F. caucana* and *F. corollata* occurs along the high ridge of the Cordillera Central on slopes of Volcán Puracé and in the Páramo de Las Papas area. *Fuchsia caucana* is only found on the eastern slopes, and *F. corollata* grows mostly on the western slopes; where they approach each other near the ridge of the cordillera, widely variable local populations are found with reduced leaves and floral tubes that are often longer than either of the

supposed parental species, but with intermediate petal size. These populations are discussed in greater detail under *F. corollata*.

25. Fuchsia ayavacensis Humboldt, Bonpland & Kunth, Nov. Gen. Pl. 6:107. 1823. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):549. 1941, pro parte. Munz, Proc. Calif. Acad. Sci. IV. 25:21. 1943, pro parte; Opera Bot., Ser. B, 3:11. 1974, pro parte. TYPE: Peru, Dept. Piura, near Ayabaca, ca. 2,850 m, Aug. 1802, *Alexander von Humboldt & Aimé Bonpland* (P, holotype, not seen; photograph, F; microfiche, MO).

Fuchsia townsendii I. M. Johnston, Contr. Gray Herb. 75:33. 1925. TYPE: Ecuador, Prov. Loja, Sabiango Hill, 26 Nov. 1910, *Charles H. T. Townsend A93* (US, holotype; photographs, NY, UC; fragment, GH).

Fuchsia asplundii J. F. Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4):548. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:37, *pl. 4, fig. 24*. 1943. TYPE: Peru, Dept. Piura, Prov. Huancabamba, above Palambla, 3,000 m, April 1912, *August Weberbauer 6054* (F, holotype; photographs, NY, POM, UC; G, GH, US, isotypes).

Suberect to scandent shrubs 1–4 m tall with flexuous branches to several m long when scandent. Young growth densely canescent-strigose or hirtellous with whitish hairs, older portions strigose to hirtellous; older branches with brown, exfoliating bark. Leaves mostly ternate, occasionally quaternate, membranous, oblong to elliptic or narrowly elliptic-oblanceolate, acute at the base, acute to subacuminate at the apex, 6–15(–18) cm long, 2.2–5(–7) cm wide, matte green and strigillose above, paler and strigose below, sometimes red-tinged; secondary veins 7–12 on either side of the midvein, at times reddish below; margin subentire to denticulate. Petioles 6–20(–30) mm long. Stipules lanceolate to triangular, 1.5–2 mm long, mostly deciduous. Flowers axillary at branch tips. Pedicels 6–25(–50) mm long, drooping. Ovary ellipsoid, 6–8 mm long, 2–3 mm thick. Floral tube narrowly funnelform, (35–)40–55 mm long, 3–3.5 mm wide and bulbous at the base, narrowed to 2–2.5 mm wide above the nectary and gradually widened above until 5–8 mm wide at the rim, subtetragonous in transection, strigose outside, pilose inside in lower ½. Sepals lanceolate, acuminate, 10–20 mm long, 4–6 mm wide, spreading to divergent at anthesis. Tube and sepals orange red. Petals orange red, broadly elliptic-ovate, rounded to subacute at the apex, 7–11 long, 5.5–8 mm wide, mostly about half as long as the sepals. Nectary unlobed or shallowly 4-lobed, 1.5–2 mm high. Filaments light red, 8–11 mm and 5–8 mm long; anthers oblong, 2.5–3 mm long, ca. 2 mm wide, white. Style light red, pilose in lower ½; stigma subobconic, 4-cleft apically, ca. 3 mm long, 3–4 mm wide, light red. Berry ellipsoid, 16–20 mm long, 8–10 mm thick, strigose, reddish; seeds 1.3–1.6 mm long, 0.8–1.1 mm wide. Gametic chromosome number $n = 11$.

Distribution: Depts. Cajamarca and Piura of northern Peru and southernmost Loja Prov. of southern Ecuador; scattered to locally frequent shrubs in secondary woods, cut-over slopes, and in thickets of moist montane forest; 1,900–3,200 m (Fig. 59).

Representative specimens examined: PERU, CAJAMARCA: between Cascas and Contumazá, *Berry & Escobar 3601* (MO, USM); Hacienda Taulis, between the Casa Hacienda and Palmito, Prov. Hualgayoc, *Hutchison & Bismark 6401* (F, G, LE, MICH, MO, NY, RSA, UC, US, USM); Socotá to San Andrés, *López & Sagástegui 5372* (MO); Prov. San Miguel, *Weberbauer 3903* (G). PIURA: 5 km

above Canchaque on road to Huancabamba, *Berry & Escobar 3630* (MO, USM); 38 km above Canchaque to Huancabamba, just below summit of road, *Hutchison & Wright 6577* (RSA, UC, USM); Bajada de Ayabaca to El Puente, *Ochoa 1782* (DS); Ciénaga Larga, Huancabamba to Cuello del Indio, *Sagástegiu et al. 8526* (MO); Ayabaca, *Soukup 4349* (US).

This is the southernmost member of the *Fuchsia petiolaris* species group. Munz (1943, 1974) confused it with *F. ampliata,* which occurs in central Ecuador and has much larger, rounder petals, wider floral tubes, and strongly reflexed sepals. *Fuchsia vulcanica* can also be confused with this species, but it generally has smaller leaves with shorter petioles and larger, wider petals. *Fuchsia ayavacensis* is characterized by its large, dull leaves with whitish, strigose-hirtellous pubescence and its often scrambling habit with long, flexuous branches. It has not been found to occur sympatrically with any other species in the section, and it is the only species centered in the relatively dry Cordillera Occidental of Peru. It grows there is moist scrub thickets and in the southernmost remnants of cloud forest on the west side of the Andes.

26. Fuchsia vulcanica André, Rev. Hort. 60:233, 268. 1888. TYPE: Colombia, Dept. Nariño, Volcán Azufral, near Túquerres, 18 May 1876, *Édouard André 3228* (K, holotype; photograph, MO).

Fuchsia hitchcockii I. M. Johnston, Contr. Gray Herb. 75:33. 1925. TYPE: Ecuador, Prov. Azuay, between Oña and Cuenca, 2,700–3,300 m, 9–10 Sept. 1923, *Albert S. Hitchcock 21603* (GH, holotype; NY, US, isotypes).

Fuchsia ayavacensis sensu Munz, Proc. Calif. Acad. Sci. IV. 25:32. 1943, pro parte; Opera Bot., Ser. B, 3:11. 1974, pro parte.

Fuchsia canescens sensu Munz, Proc. Calif. Acad. Sci. IV. 25:26. 1943, pro parte; Opera Bot., Ser. B, 3:12. 1974, pro parte.

Erect to scandent shrubs 0.4–3.5 m tall, sometimes semi-epiphytic on mossy tree trunks. Branchlets terete, 1.5–3 mm thick, densely hirsute to hirtellous or strigillose, usually with erect, white to tan hairs; older stems 3–10 mm thick with exfoliating bark. Leaves 3–5-verticillate, mostly ternate or quaternate, firmly membranous to subcoriaceous, narrowly to broadly elliptic to obovate, acute to obtuse at both ends, 2–5(–10) cm long, (0.6–)1–2.5(–4) cm wide, matte to subnitid green and usually strigose above, lighter green and hirsute to strigose below; secondary veins 3–8(–11) on either side of the midvein, often red below; margin subentire to denticulate. Petioles pubescent, 2–10(–20) mm long. Stipules narrowly lanceolate, 1.5–2.5 mm long, 0.3–0.7 mm wide, deciduous. Flowers generally fewer than 12 per branch, axillary and pendant. Pedicels pubescent, 5–25(–40) mm long. Ovary ovoid-ellipsoid, strongly tetragonous, 6–9 mm long, 2–3.5 mm thick, hirsute to strigose, green to dull red. Floral tube narrowly funnelform, (32–)36–50(–60) mm long, 3–4 mm wide and somewhat bulbous at the base, narrowed to 2–3.5 mm wide above the nectary, then gradually widened or slightly ampliate near the middle until 6–10 mm wide at the rim, hirsute to strigose or subglabrous outside, pilose inside for most its length. Sepals (narrowly) lanceolate, acute to subacuminate at the apex, (10–)13–20(–23) mm long, 3.5–5 mm wide, spreading to divergent at anthesis. Tube and sepals subnitid scarlet, pink, or orange red, sepals sometimes dull, green-tipped. Petals red, orbicular to obovate or broadly elliptic, rounded to (broadly) acute at the apex, (8–)9–15 mm long, (6–)8–13 mm wide, spreading to divergent at anthesis. Nectary unlobed or shal-

lowly 4-lobed, 1.5–2 mm high. Filaments red, 8–12 mm and 6–9 mm long; anthers oblong, 3–4 mm long, 1.5–2 mm wide, cream. Style red, villous for most its length; stigma conic-globose, slightly 4-cleft apically, 2–3.5 mm long, 1.5–4 mm wide, red. Berry tetragonous before maturity, subglobose to ellipsoid when ripe, 11–15 mm long, 7–9 mm thick, red purple; seeds tan, 1.8–2.5 mm long, 0.9–1.2 mm wide. Gametic chromosome number $n = 11(?), 22$.

Distribution: Southern Colombia and Ecuador. Along the Cordillera Occidental from Nariño, Colombia to Cotopaxi, Ecuador, in elfin forest near tree line, 3,400–4,000 m; on the Cordillera Central (eastern escarpment of the Ecuadorian Andes) from Napo to Chimborazo, from tree line at 3,900 m to 2,500 m in cloud forest; and in the mountains of Azuay and Cañar from tree line to upper cloud forest, 2,850–3,400 m (Fig. 59).

Representative specimens examined: COLOMBIA, NARIÑO: Volcán Azufral, *André s.n.*, (K); Volcán Galera, near Pasto, *Barclay 4637* (COL); La Laguna, Mun. Cumbal, *Benavides 993* (PSO); NW slopes Volcán Chiles, *Ewan 16093* (POM); Volcán Cumbal, *Vogel 259* (U), *von Sneidern in 1941* (S). ECUADOR, AZUAY: Páramos de Silván, *Barclay & Juajibioy 8403* (RSA); 13–18 km from Cuenca on road past Sayausí, *Berry & Escobar 3184* (MO), *3187* (MO, QCA), *3188* (MO); 35 km S of Cuenca on road to Oña, *Berry & Escobar 3190* (MO, QCA); along Río Yanucay above San Joaquín, road to Laguna Soldado, *Berry & Escobar 3212* (MO, QCA), *3213* (MO), *3214* (MO), *3225* (MO, QCA); Yanasacha, Parroquía Baños, *Boeke 621* (MO); road Cuenca-Angas, near Angas, *Boeke 654* (MO); Páramo de Tinajillas, 30–50 km S of Cuenca, *Camp E-462* (NY, RSA), *E-2107* (NY, RSA), *E-2108* (NY, RSA); along Río Matadero, W of Cuenca, *Camp E-1988* (NY, RSA, U); N of Paute, *Camp 2590* (NY, RSA, VEN); 1–8 km N of Sevilla de Oro, *Camp 4257* (NY, RSA), *E-4672* (COL, G, MO, NY, P, RSA, S, US, VEN); Quebradas of the Río Collay, 3–8 km N of Sevilla de Oro, *Camp 4994* (G, MO, NY, RSA, UC, US); El Pan, *Harling 1228* (NY, S); 10 km S of Cumbe, *Harling 5658* (NY, S); 10–12 km N of Sevilla de Oro, *Øllgaard & Balslev 9366* (AAU, MO), *9374* (AAU, MO); near Laguna Sorocucho, *Prescott 827* (DS, NY), *Scolnik 1461* (RSA); Río Machangara, *Sparre 18561* (S), *18601* (S), *18664* (S). CAÑAR: above Biblián on road to Cañar, *Berry & Excobar 3227* (MO, QCA), *3228* (MO, QCA), *Harling 6296* (NY, S), *Harling et al. 8614* (RSA). CARCHI: Páramos del Angel, near Voladero, *Barclay & Juajibioy 9396* (RSA), *Penland & Summers 915* (F, GH, POM); base of Volcán Chiles, ca. 12 km W of Tufiño, *Berry 3156* (MO, QCA), *Øllgaard & Balslev 8398* (AAU); near El Angel, *Popenoe 1260* (NA); Páramo El Angel, *Sparre 14148* (S). CHIMBORAZO: Cordillera Oriental, between Alao & Cushnipaccha, *Acosta Solis 7201* (F), *7214* (F). COTOPAXI: 17 km above Pilaló, road to Latacunga, *Berry & Berry 2539* (MO), *2540* (MO); timberline on Pilaló-Latacunga road, *Holm-Nielsen & Jeppesen 1396* (AAU, S), *Holm-Nielsen et al. 3335* (AAU, S). IMBABURA: Laguna de Mojanda, *Øllgaard & Balslev 8779* (AAU). NAPO: between Oyacachi and Comenia, *Acosta-Solis 11166* (F); Cuyuja, *Balslev & Madsen 10469* (AAU), *10522* (AAU); ca. 5 km above Papallacta to Quito, *Berry & Berry 2521* (MO); Km 215 of Quito-Baeza road just above Lago Papallacta, *Berry & Berry 2523* (MO); 2–6 km below Papallacta, *Berry & Berry 2525* (MO), *2526* (MO), *Gentry 12401* (MO, US); just above town of Papallacta, *Berry & Escobar 3245* (MO); Lago San Marcos, E of Cayambe, *Cazalet & Pennington 5312* (NY, UC, US); Quebrada Chalpichio, ca. Km 204 E of Papallacta, *Croat 49412* (MO); Los Corrales, near Papallacta, *Grubb et al. 208A* (NY 2 sheets); below Papallacta, *Harling 3994* (NY, S); 4 km W of Papallacta, *Holm-Nielsen et al. 6785* (AAU, MO, NY, S); between Cuyuja and Papallacta, 10 km E of Papallacta, *Holm-Nielsen et al. 6834* (AAU, NY, S); Laguna de Papallacta, *Øllgaard & Balslev 8036* (AAU); ca. 7 km W of Papallacta, *MacBryde & Dwyer 1240* (MO, QCA); just W of Papallacta, *Plowman et al. 3870* (GH, K, MO, S); Río Papallacta, Station IV, *Prescott 1276* (MSC); Dos Arroyos, ca. 5 km NW of Laguna Norte de Papallacta, *Sparre 15021* (S); Río Calpi on Baeza-Papallacta road, *Sparre 15949* (S); Papallacta, *Sparre 17704* (S). PICHINCHA: E part of Haciendas Pedregal and Yanurcu, Chaparro de Sebritana, *Acosta-Solis 8353* (F); NW side of Volcán Pichincha, Yanacocha trail, *Luteyn et al. 5685* (MO). TUNGURAHUA: Llanganati mountains, ridge between Río Tope and Río Golpe, *Edwards 164* (K); Páramo de Minza, Minza Chica, *Penland et al. 337* (F, GH, POM).

Probable hybrids *Fuchsia vulcanica* × *F. ampliata*: ECUADOR, COTOPAXI: above Pilaló, 2,800 m, *Barclay & Juajibioy 8076-A* (RSA); 13 km above Pilaló on Quevedo-Latacunga road, ca. 3,300 m, *Berry & Berry 2541* (MO), *2542* (MO), *2543* (MO), *2544* (MO), *2545* (MO), *2546* (MO), *2547* (MO);

12 km E of Pilaló, *Escobar 1100* (MO); Prov. Cotopaxi, *Gilmartin 44* (MO); Pilaló-Latacunga road at timberline, 3,400 m, *Holm-Nielsen & Jeppesen 1396* (DS), *1397* (AAU, DS); Quevedo-Latacunga road, above Pilaló, 3,200–3,300 m, *Holm-Nielsen et al. 3268* (COL, MO, NY, S).

This species is part of the high elevation *Fuchsia petiolaris* species group of the northern Andes. It and *Fuchsia ampliata* are closely related and distinct from the other species in their generally rotund petals and coarse, usually dense pubescence. *Fuchsia vulcanica* can be distinguished from *F. ampliata* by its non-reflexed sepals, strongly tetragonous ovaries, smaller leaves, and shorter petioles and pedicels.

Fuchsia vulcanica is treated here as a widely polymorphic species. Intensive field work and cytological examination of more populations is badly needed and may in the future lead to the recognition of additional taxa, but the extent of variation within most parts of the range is such that no consistent morphological differences can be found to separate distinct taxa at this time.

The most uniform populations occur around the type locality in southern Colombia and northern Ecuador, where plants are all densely hirsute, with leaves less than 35 mm long, and pedicels less than 8 mm long. These plants occur only at or near treeline on the upper slopes of volcanic peaks. A possible diploid count of n = ca. 11 was obtained from this area from *Berry 3156*. Along the same mountain range, but further south in Imbabura and Pichincha, plants are found with shorter, hirtellous pubescence and slightly larger leaves 3–6 cm long.

The southernmost populations from Azuay and Cañar are apparently all tetraploid. Four tetraploid counts were obtained from two different populations (see Table 4). In addition, triporate pollen grains, which often indicate polyploidy in the genus, have been found in representatives of different localities in this area, including *Harling 1228* (NY, S; El Pan), *Berry & Escobar 3225* (MO, QCA; above San Joaquín, road Cuenca-Laguna Soldado), *Øllgaard & Balslev 9374* (AAU, MO; 10–12 km N of Sevilla de Oro), and *Harling et al. 8614* (RSA; between Biblián and Cañar). Most plants from Azuay have somewhat smaller and thinner flowers than those found in the northern Provinces. Pubescence varies widely in these populations from densely hirsute to hirtellous, and the petals are particularly variable, from orbicular to elliptic and acute-tipped.

The type of *F. hitchcockii* is unusual in its long floral tubes (ca. 60 mm long). It represents the extreme of variability in this group, with petals half as long as the sepals and pedicels 3–4 cm long. Its hirsute pubescence and round petals are characteristic of *F. vulcanica,* however, and other collections from the same area are variable, but generally closer to the average values of morphological characters for this species.

There are two areas where *F. vulcanica* intergrades extensively with *F. ampliata* or else shows a great deal of polymorphism over an altitudinal gradient. In the Cordillera de Zumbagua, above Pilaló in Prov. Cotopaxi, *F. vulcanica* is found locally near treeline, ca. 3,450–3,500 m, and *F. ampliata* has been found in cloud forest around 2,850 m, but both are infrequent. In between, a wide range of intermediate forms were found; these collections are listed separately at the end of the specimens citation as probable hybrids of *F. vulcanica* × *F. ampliata*. In July 1977, *Berry & Berry 2541* to *2547* were collected from a rock pile that had been made by roadbuilding machinery. This population appeared to be a

hybrid swarm between the above two species, as shown by the wide variation in the degree of sepal reflexion, leaf size and texture, and pubescence. No significant reduction in pollen stainability occurs in the intermediate forms, however, which seems to confirm the close affinity of these two species. In 1979, two years after the initial visit, this population had been destroyed by road cleaning crews. Such repeated disturbance and rapid turnover of local populations and the tendency of *F. ampliata* to grow in higher and drier sites than the Zumbagua cloud forest are likely major factors in the probable breakdown of isolating mechanisms between *F. vulcanica* and *F. ampliata* in Cotopaxi.

The second area where considerable variability involving *F. vulcanica* occurs is in Napo, on the road from Quito to Baeza on the eastern slopes of the Andes. Typical, small-leaved, high elevation forms of *F. vulcanica* occur about 5 km above the town of Papallacta near treeline at 3,700 m. As one descends first to the town of Papallacta at ca. 3,300 m, then down as low as 2,500 m in cloud forest to the east of Papallacta, considerably larger leaved plants are found along with greater variability in pedicel length and degree of sepal reflexion. *Berry & Berry 2528* (MO; ca. 12 km east of Papallacta, 2,600 m) is the extreme of leaf variation, with blades 10 cm long and 4 cm wide, with 9 secondary veins on each side of the blade. *MacBryde 875* (MO; W end of Lago Papallacta, 3,300 m) has some pedicels 4 cm long and floral tubes 10–13 mm wide at the rim, both beyond the normal range of variability for *F. vulcanica*. All these collections share the 3–4-verticillate, short-petiolate leaves, hirtellous pubescence, and round petals of *F. vulcanica*, however. *Asplund 18239* (S; Papallacta, 3,000 m) is a large-leaved form that apparently has reflexed sepals. This points to possible introgression with *F. ampliata*, but that species is not known from the eastern slopes of the Andes in Ecuador. A gametic chromosome count of n = ca. 22 was obtained from *Berry & Escobar 3245* (MO, QCA; Papallacta). More intensive sampling and cytological study of plants from this area will be necessary to understand the dynamics of these populations better.

Besides *F. ampliata*, *F. vulcanica* occurs sympatrically with *F. loxensis* in Azuay and with *F. pallescens* at its lower altitudinal limits in Napo.

27. Fuchsia ampliata Bentham, Pl. Hartw. 178. 1845. Baill., Hist. Pl. 6:467, *fig. 439*. 1877. Hook., Bot. Mag. *t. 6839*. 1885. TYPE: Ecuador, Prov. Pichincha, slopes of Volcán Pichincha, ca. 3,000 m, 1841–1843, *Theodor Hartweg 988* (K Bentham Herb., holotype; photograph, MO; BM, BR, BREM, CGE 2 sheets, F, G, K Hooker Herb., OXF, P, W 2 sheets, isotypes). Fig. 23.

Fuchsia ayavacensis sensu Munz, Proc. Calif. Acad. Sci. IV. 25:32, *pl. 3, fig. 18*. 1943, pro parte; Opera Bot., Ser. B, 3:12. 1974, pro parte.
Fuchsia canescens sensu Munz, Opera Bot., Ser. B, 3:12. 1974, pro parte.

Erect to scandent shrubs 1–3 m tall with mostly ascending branches. Young growth conspicuously canescent to hirtellous with white hairs; branchlets 2–3 mm thick, hirtellous to densely strigose, green to dull purple; older branches dull ash gray. Leaves ternate or occasionally quaternate, often drooping, membranous, (narrowly) elliptic to lanceolate, acute to narrowly cuneate at the base, acute to subacuminate at the apex, 4–9(–12) cm long, 1.5–4 cm wide, matte green

and strigose above, pale green and strigose-villous below with red purple veins; secondary veins 5–9(–11) on either side of the midvein; margin subentire to denticulate. Petioles strigose, 7–20 mm long, usually dull purple. Stipules lance-linear, 3–5 mm long, 0.5–1 mm wide, subpersistent. Flowers axillary and pendant, generally few. Pedicels stout, 1–2 mm thick, 15–35(–50) mm long, strigose. Ovary ovoid, usually constricted near the apex, 6–8 mm long, 3–4 mm wide, canescent-hirtellous and slightly furrowed. Floral tube funnelform, usually dilated above the middle, (32–)40–50(–65) mm long, 3–4.5 mm wide and bulbous at the base, tapered to 2–3(–4) mm wide in lower ⅓, widened above until (6–)8–14 mm wide at the rim, strigose outside, villous inside for lower ½–¾. Sepals lanceolate, narrowly acute at the apex, 16–23(–28) mm long, 6–8 mm wide, with a narrow, tapered tip in bud, fully reflexed soon after anthesis. Tube and sepals bright scarlet to orange red. Petals red to orange red, rotund to orbicular or very broadly ovate, (10–)13–18 mm long, (9–)10–16 mm wide, rounded to obtuse at the apex, erect to suberect at anthesis. Nectary green, shallowly 4–8-lobed, ca. 2 mm high. Filaments red or orange, 10–18 mm and 8–13 mm long; anthers oblong, ca. 4 mm long, 2–3 mm wide, cream. Style red, densely villous from the base to the rim of the tube; stigma globose to subclavate, slightly 4-cleft apically, 2–4 mm long, 2–4 mm wide, red. Berry ellipsoid, usually ± tetragonous before maturity, slightly verrucose, 14–16 mm long, ca. 8 mm thick, red; seeds tan, 1.8–2.1 mm long, 0.8–1.2 mm wide. Gametic chromosome number $n = 11$.

Distribution: Ecuador, along the Cordillera Occidental from Imbabura to Bolivar and one collection from the Nariño-Putumayo border in southern Colombia; shrubs in hedgerows on dry slopes, near streams or in upper elevation cloud forest, (2,850–)3,000–3,500 m (Fig. 60).

Representative specimens examined: COLOMBIA, PUTUMAYO: S side of Laguna La Cocha, Páramo de Santa Lucía, source of Río Alisales, *Cuatrecasas 11884* (COL). ECUADOR, BOLIVAR: Simiatug, Hacienda Talahua, *Penland et al. 623* (F, GH, POM). COTOPAXI: Quevedo-Latacunga road, above Pilaló, 2850 m, *Holm-Nielsen et al. 3274* (AAU, NY, S). IMBABURA: Bosque Andino "Rosaspamba," E side of Mojanda, *Acosta-Solis 8104* (F); ca. 8 km W of Laguna Cuicocha on road to Intá, *Berry 3169* (MO, QCA); ridge of Moinala, SW of Volcán Cotacachi, *Owenby 2646* (COL, MO, RSA, US). PICHINCHA: Corazón, *André K.819* (F, K, NY); ca. 9 km W of Chillogallo to Chiriboga, *Berry & Escobar 3234* (MO, QCA); Pichincha, *Jameson in 1851* (BM, CGE, G, OXF, US), *Humboldt & Bonpland 3115* (F, P); Volcán Pichincha, *Mexia 7654* (BH, UC, US); road from Cotocollao, near Nono, *Mexia 7661* (BM, GH, K, MO, NY, POM, S, U, UC, US).

This species can be easily recognized by its broad, firm-tubed flowers with nearly erect, round petals and fully reflexed sepals at anthesis. The plants are generally covered by a tomentum of white, strigose-villous hairs, and the styles are densely pilose up to the rim of the tube. *Fuchsia ampliata* is a member of the high elevation *F. petiolaris* species group and was confused by Munz (1943, 1974) with *F. ayavacensis* from northern Peru and southernmost Ecuador. The differences between these two species are outlined under *F. ayavacensis*. *Fuchsia ampliata* largely is restricted to areas near tree line in a small extension of the Cordillera Occidental in central Ecuador, mostly on the drier eastern slopes facing the Central Valley of Ecuador. One disjunct collection is known from the eastern slopes of the Cordillera Central in southern Colombia, however. In Cotopaxi, Ecuador, above Pilaló, it occurs in moister cloud forest but is apparently quite rare. There, it hybridizes extensively with the closely related *F. vulcanica*, pro-

ducing local hybrid swarms. These are discussed more fully under *F. vulcanica*. *Fuchsia ampliata* also occurs sympatrically with *F. dependens* and *F. sessilifolia* in a few localities.

28. Fuchsia venusta Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 6:105. 1823. Planch., Fl. Serres Jard. Eur. 5: *t. 538*. 1849; Rev. Hort. III. 4:241, *t.* 1850. Moore & Aynes, Gard. Mag. Bot. 2:36, *fig. 2*. 1850. Lindl. & Paxt., Paxton's Fl. Gard. 1:79, *fig. 57*. 1850. Anon., J. Hort. Pract. Gard. III. 49:243, *t.* 1904. *Fuchsia venusta* var. *typica* Munz, Proc. Calif. Acad. Sci. IV. 25:39, *pl. 5, fig. 26*. 1943. Based on *F. venusta* HBK. TYPE: Colombia, Dept. Cundinamarca, near Guayavalito, July–Sept. 1801, *Alexander von Humboldt & Aimé Bonpland* (P, holotype, not seen; photographs, F, GH; microfiche, MO; P, isotype). Fig. 24.

Fuchsia killipii I. M. Johnston, Contr. Gray Herb. 81:94. 1928. Munz, Proc. Calif. Acad. Sci. IV. 25:52, *pl. 8, fig. 41*. 1943. TYPE: Colombia, Dept. Santander, Río Suratá, above Suratá, 2,000–2,300 m, 5–6 Jan. 1927, *Ellsworth P. Killip & Albert C. Smith 16695* (GH, holotype; photographs, POM, UC; NY, US, isotypes).

Fuchsia venusta var. *huilensis* Munz, Proc. Calif. Acad. Sci. IV. 25:39. 1943. TYPE: Colombia, Dept. Huila, Cordillera Oriental, E of Neiva, 1,800–2,300 m, 1–8 Aug. 1917, *Henry H. Rusby & Francis W. Pennell 874* (NY, holotype; photographs, POM, UC; F, GH, MO, US, isotypes).

Fuchsia meridensis Steyermark, Fieldiana Bot. 28:439. 1952. TYPE: Venezuela, Edo. Mérida, between La Azulita and La Trampa, road to Lagunillas, 1,280–2,285 m, 27 Aug. 1944, *Julian A. Steyermark 56162* (F 1368909, holotype; NY, isotype).

Erect to scandent shrubs 1–3 m tall or lianas to 10 m above ground, with suberect or long, flexuous-pendant branches to several m long. Branchlets terete to subtriangular, 2–6 mm thick, minutely puberulent to finely hirtellous, dull wine red to bluish purple; older branches 10–40 mm thick, with tan, exfoliating bark. Leaves ternate, rarely opposite or quaternate, firmly membranous to subcoriaceous, elliptic, rounded to acute at the base, acute to subacuminate at the apex, 5–11.5 cm long, 1.5–4.5 cm wide, glossy dark green and subglabrous above, glossy pale green and subglabrous to pubescent along the nerves below; secondary veins 7–12 on either side of the midvein, impressed above, subelevated below; margin subentire. Petioles puberulent or strigillose, 4–10(–12) mm long, wine red. Stipules lance-deltoid, 1–1.5 mm long, ca. 0.4 mm wide, subulate at the apex, deciduous. Flowers axillary in uppermost leaf axils or subracemose at branch tips; when subracemose, rachis 2–4 cm long, subtending leaves usually deciduous. Pedicels slender to filiform, ascending to divergent in bud, arching or drooping by anthesis, (10–)15–30(–60) mm long, glabrous to pubescent. Ovary oblong to ellipsoid, 4–8 mm long, 2–3 mm thick. Floral tube narrowly funnelform, (30–)35–60 mm long, 2.5–4.5 mm wide and slightly bulbous at the base, narrowed to 2–4 mm wide above the nectary and gradually widened above until 5–10 mm wide at the rim, subglabrous to puberulent outside, pilose inside for most of length. Sepals lanceolate, 14–20 mm long, 4–7 mm wide, acute to acuminate at the apex, sometimes pubescent within, subulate in bud for 1–2 mm, spreading to divergent at anthesis. Tube lustrous orange red, at times greenish in bud; sepals orange red, often green-tipped in bud. Petals orange to orange red, oblanceolate, 15–22 mm long, 3–6 mm wide, undulate to crispate-margined, abruptly acute at the apex, strongly spreading and recurved at anthesis, with dorsal hairs occasionally pres-

ent along the midvein. Nectary green, unlobed to shallowly 4-lobed, ca. 2 mm high. Filaments light red, 10–15 mm and 8–11 mm long; anthers oblong, 2.5–3.5 mm long, 1.5–2 mm wide, cream to pale yellow. Style densely villous from the base to the rim of the tube, light red; stigma subglobose, 4-cleft apically, 2–3 mm long, 2–3 mm wide, dull white to orange red, exserted 3–15 mm beyond the anthers. Berry ellipsoid-oblong to subglobose, 8–20 mm long, 6–10 mm thick, lustrous dull green to dark purple; seeds tan, 1.5–2 mm long, 0.8–1.5 mm wide. Gametic chromosome number $n = 11$.

Distribution: Colombia and Venezuela. Locally frequent to scattered shrubs or lianas along forest edges, streamsides, thickets or in trees of mid-elevation cloud forest; in Venezuela, from Mérida to Táchira; in Colombia in the Cordillera Oriental from Santander to Huila, and in the Cordillera Central in Tolima; 1,800–2,700 m (Fig. 60).

Representative specimens examined: VENEZUELA, MÉRIDA: La Carbonera, *Aristeguieta 2847* (NY, VEN); La Loma de la Vagabunda, near El Morro, between El Morro and Aricagua, *Badillo 6563* (MY); Quebrada de La Mucuy, towards El Volcán, *Bernardi 280* (MER, NY); La Mucuy, *Bernardi 306* (MER, NY, VEN); Alto de Monte Zerpa, *Bernardi 664* (NY); El Paramito, between Mérida and La Carbonera, *Berry & Dugarte 2507* (MER, MERF, MO), *Berry 3450* (MO, VEN); ½ km below La Trampa, *Berry & Centeno 2511* (MER, MERF, MO); 23 km above La Azulita on road to La Trampa, *Berry & Centeno 2512* (MER, MERF, MO); 17 km E of Zumbador to Queniquea, *Berry 3422* (MO, VEN); La Mucuy to Mesa de los Pinos, *Berry 3431* (MO, VEN), *Berry in 1980* (MO), *3433* (MO, VEN); 3–5 km below San Eusebio, road to La Azulita, *Berry 3542* (MO, VEN), *3455* (MO); Páramo de Aricagua, *Jahn 1029* (GH, US, VEN); Chorrera de La Gonzales-La Isla-Jají, *López-Palacios 1919* (MERF, MO); El Chorotal, *Quintero 1614* (MER); El Valle Grande, between San Javier and la Sierra de la Culata, *Ruiz-Terán & López-Figueiras 2116* (MERF, MO); El Yagrumal, above El Maciegal, ca. 10 km W of Mérida, *Ruiz-Terán et al. 12540* (MERF, MO); Bosque Experimental de San Eusebio, *Wessels-Boer 1733* (MER, MO, U, VEN). TÁCHIRA: 21 km E of El Portachuelo to Pregonero, *Berry 3292* (MO, VEN); 13 km E of Zumbador, *Berry 3302* (MO, VEN); 11–17 km W of Zumbador towards San Isidro, *Bunting 2564* (MY); Páramo el Pantano, *Charpin et al. 13459* (G); Páramo del Zumbador, *Ferrari 1171* (MY); Páramo de Angaraveca, *Jahn 129* (US, VEN); between Michelena and Boca de Monte, W of Zumbador, *Steyermark & Rabe 96805* (NY, U, VEN); 4.5 km above El Hato, ca. 30 km above Pregonero on road to Bailadores, *Tillett & Hönig 758-520* (MO). COLOMBIA, BOYACÁ: Chiquinquirá, *Ariste-Joseph A842* (US); Yanaca-Mapiri, *García-Barriga 4911* (COL, US); near Socotá, Sierra Nevada del Cocuy, *Grubb et al. 697* (COL, K); Km 307 above Pajarito, Rancherías, *Idrobo & Jaramillo 1605* (COL); near Quebrada Chorro Grande, N side Arcabuco Range, between Duitama and Charalá, *Langenheim 3614* (COL, UC, US); Finca La Saria, Corregimeinto de Virolín, *Lozano et al. 2393* (COL); Km 88 road to Pajarito, Quebrada La Rocha, *Sastre 733* (COL, MO, P); road to Barbosa, 10 km NW of Arcabuco, *Steere 7048* (BH, COL, MICH); above Corinto, road Pajarito-Sogamoso, *Uribe-Uribe 6534* (COL); Tota, *Yepes-Agredo 3339* (COL). CUNDINAMARCA: Quebrada Honda, *André in 1876* (K); Facatativá, *Ariste-Joseph A514* (US); ca. 2.5 km W of Salto de Tequendama, road to El Colegio, *Barclay et al. 3305* (COL, NA, US); just below Zipacón, *Berry 3540* (COL, MO); Km 39 of Bogotá-Sibaté-Fusagasugá road, *Berry 3548* (COL, MO); 10 km above Choachí, *Breedlove 35540* (CAS); Salto de Tequendama, *Cuatrecasas 48* (COL, F, US); Boca de Monte, *Cuatrecasas et al. 25816* (COL); Tena, *Dawe 23* (K, US); Choachí, *Dawe 350* (K, US); San Miguel and Aguabonita, *Duque-Jaramillo 3323* (CM, COL); Laguna Pedro Palo, 3 km N of Tena, *Fernández & Mora 1449* (COL); 5 km NNW of Cabrera, N and W of Río Sumapaz, *Fosberg 20982* (RSA, US); 12 km WSW of Junín, on Río Blanco, drainage of Río Sueva, *Fosberg 21479* (NY, RSA, UC, US); *21482* (RSA, US); 5 km WSW of Charquito, headwaters of Río Subia, *Fosberg 22038* (NY, RSA, US); between Pacho and Río Negro, *García-Barriga 10754* (COL, US); Sasaima, La María, *García-Barriga 12584* (COL, POM, US); Km 18 of road Mosquera-La Mesa, *Gentry 17050* (COL, MO); 12 km NW of Gachetá, Moquentina valley, *Grant 9534* (NA, RSA, US); San Fortunato, *Hartweg 995* (BM, BREM, CGE, F, G, K, LE, NY, OXF, P, W); Zipaquirá-Pacho highway, *Haught 5979* (COL, POM, US); Fómeque, toward the Páramo de Chingaza, *Huertas & Camargo 5536* (COL); Junín, Vereda La Cumbre, toward Claraval, *Huertas & Camargo 6602* (COL); above La Florida, *Idrobo & Jaramillo 2250* (COL); Las Mercedes, *Lourteig 3082* (MO); between Agua Larga and Facatativá, *Mayor 56* (Z); Dintel, *Pérez-Arbelaez & Cuatrecasas 5291* (F, COL); Zipacón, *Popenoe 1056* (NA); Santandercito-La Rambla, *Silva & Moreno 270* (COL); Santandercito, *Uribe-Uribe 1020*

TABLE 11. Distinguishing characters of *Fuchsia gehrigeri* and *F. venusta*.

	F. gehrigeri	*F. venusta*
Twig color	Light red to green	Wine red
Leaf surface	Matte	Glossy
Leaf texture	Membranous	Firmly membranous to subcoriaceous
Leaf margin	Denticulate	Entire
Petiole length	10–40 mm	4–10 mm
Flower color	Red	Orange red
Petal surface	Smooth	Undulate
Fruit shape	Ovoid-globose	Ellipsoid
Seed length	2–3 mm	1.5–2 mm

(COL, U); Pacho, *Uribe-Uribe 1718* (COL). HUILA: Batán, on Río Neiva, ca. 32 km SE of Neiva, *Fosberg 19296* (NY, RSA); Quebrada Ariari, above Galilea, 23 km ENE of Colombia, *Fosberg 19625* (RSA, US); Yucales, on Río Fortalecillas, 32 km E of Neiva, *Fosberg 19744* (RSA, US); E of Neiva, *Rusby & Pennell 641* (GH, MO, NY, US); Balsillas, on Río Balsillas, *Rusby & Pennell 722* (GH, NY, US). SANTANDER: La Baja, *Funck & Schlim 1306* (BM, CGE, F, G, LE, OXF, P, W); above Suratá, *Killip & Smith 16604* (A, US); vicinity of La Baja, *Killip & Smith 16776* (A, F, GH, NY, S, US); vicinity of Charta, *Killip & Smith 18854* (A, GH, NY, US). TOLIMA: 24 km W of Fresno to Manizales, *Berry 3551* (COL, MO); between Líbano and Murillo, *Escobar 1008* (MO); Líbano, *Pennell 3197* (GH, NY, US).

Fuchsia venusta is one of few species that often climb up trees, with its long, flexuous branches (Fig. 3). It also can grow as an upright shrub, however. It is distinguished by its ternate, short-petiolate, elliptic leaves that are glossy on both surfaces and the wine red to dull bluish purple stems. The flowers are axillary to subracemose, with orange tubes, green-tipped sepals, and recurved, undulate-crispate petals. It is closely related to *F. rivularis* from northern Peru. That species, however, has mostly quaternate leaves, more secondary veins, and mostly spreading sepal tips in bud. *Fuchsia gehrigeri* is another related species that is sympatric and can be confused with *F. venusta*; a list of their distinguishing characters is given in Table 11.

Considerable variation in pubescence, leaf texture, and amount of green coloration in the tube and sepals occurs between different populations of *Fuchsia venusta*. Along the edges of the Bogotá Plateau where this species is common, localized variation in the above characters is found. Plants near the Salto de Tequendama have subcoriaceous leaves and thick stems with erect, hirtellous pubescence, but populations nearby at Zipacón and Aguabonita on the old Bogotá-Fusagasugá road are typically subglabrous with membranous leaves. However, plants from opposite ends of the range, in Huila, Colombia and Mérida, Venezuela, often show little morphological differentiation.

Populations from northern Santander were described by Johnston as *Fuchsia killipii*. Compared to other populations of *F. venusta*, these plants have more numerous flowers in generally tightly clustered groups and smaller, globose fruits. I could not find populations from this area during field studies in Santander, but the cited collections appear to be localized variants of *F. venusta* because of their shrubby to climbing habit, ternate, glossy leaves, pilose styles, and the frequent hairs on the petals and sepals.

There are a few localized populations of *F. venusta* in Dept. Tolima on the

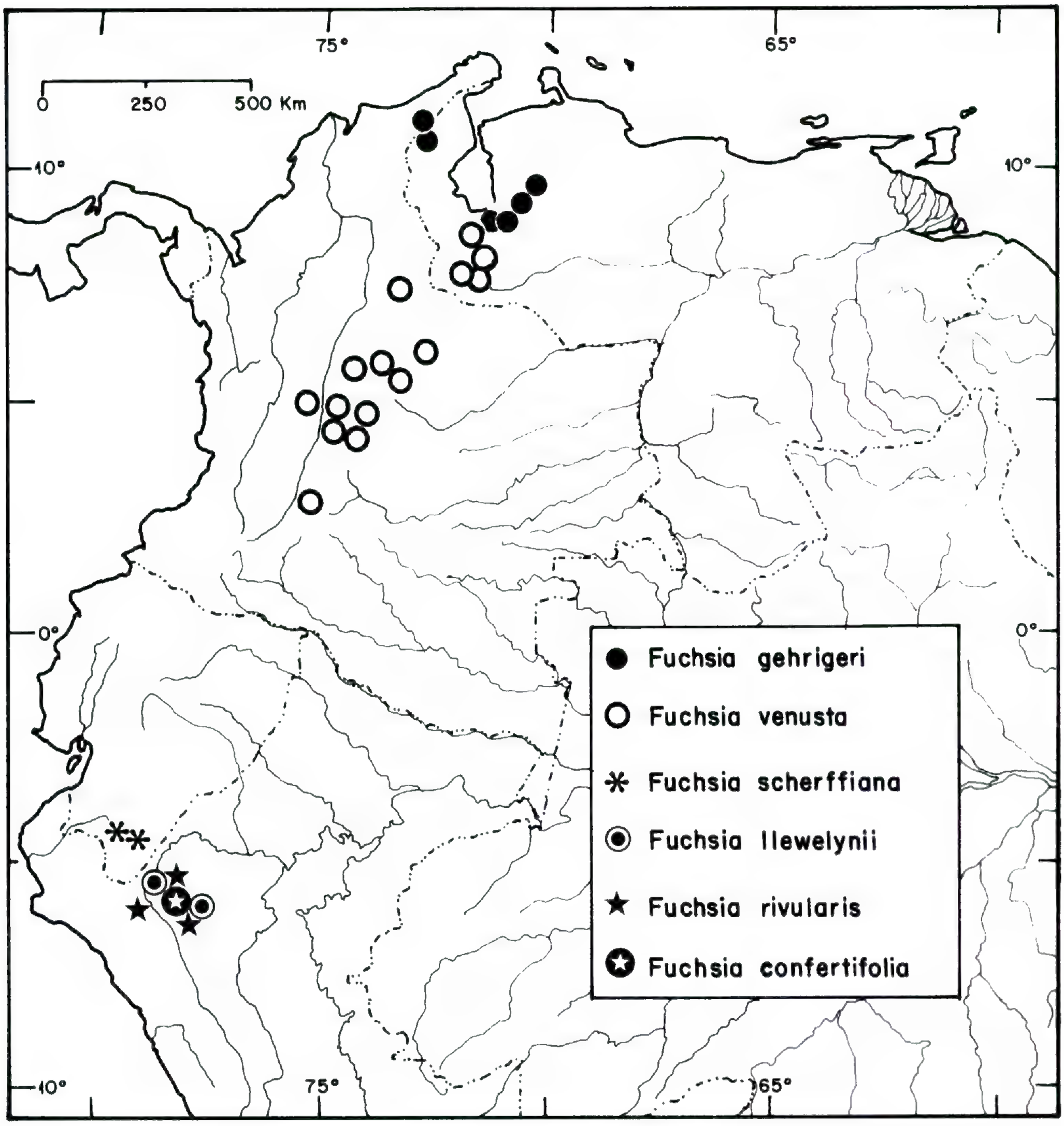


FIGURE 60. Distribution of the *Fuchsia venusta* species group.

eastern slopes of the Cordillera Central at the latitude of the Bogotá Plateau; plants probably spread there from the Cordillera Oriental, the same as with *F. hirtella*, *F. nigricans*, and *F. petiolaris*.

Fuchsia venusta occurs sympatrically with *F. gehrigeri*, *F. hirtella*, *F. nigricans*, and *F. verrucosa*. It apparently hybridizes with *F. gehrigeri* in Mérida and Táchira, Venezuela. Hybrids with *F. hirtella* were collected in Cundinamarca, Colombia, along the old Bogotá-Fusagasugá road. In both these cases, the putative hybrids occur at the upper altitudinal limit of *F. venusta* and the lower limit of *F. hirtella* and *F. gehrigeri* (Fig. 6). Hybrids between *F. venusta* and *F. nigricans* are relatively common in Venezuela. Further analysis of these hybrids is included in the discussion of *F. gehrigeri*, *F. hirtella*, and *F. nigricans*.

29. Fuchsia rivularis J. F. Macbride, Candollea 8:24. 1940; Field Mus. Nat. Hist., Bot. Ser. 13(4):562. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:27. 1943. TYPE: Peru, Dept. Amazonas, Chachapoyas, 1830–1841, *Andrew Mathews* (G-BOIS, lectotype, here designated; photograph, MO; G-DEL, isolectotype).

Fuchsia woytkowskii J. F. Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4):566. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:25, *pl. 2, fig. 11*. 1943. TYPE: Peru, Dept. Amazonas, Almirante, 1,900 m, *Felix Woytkowski 38* (F, holotype; photographs, NY, UC).

Scandent shrubs or lianas to 10 m above ground, with long, flexuous-arcuate, mostly unbranched shoots to several m long. Branchlets and young growth subglabrous to puberulent, older branches pilose or puberulent, glabrescent with age, with subnitid, red purple bark exfoliating in wide strips. Leaves ternate or mostly quaternate, subcoriaceous, narrowly elliptic to elliptic, acute to obtuse at the base, narrowly acute to obtuse or subacuminate at the apex, 5–9 cm long, 2–5 cm wide, nitid dark green and subglabrous above, paler green and subglabrous to pilose below; secondary veins 13–15 on either side of the midvein, midrib elevated below; margin subentire to glandular-denticulate. Petioles stout, pilose, 3–6 mm long. Stipules triangular-lanceolate, 2–3 mm long, 0.8–1.3 mm wide, thick at the base, spreading, subpersistent. Flowers few and pendant in uppermost leaf axils. Pedicels drooping to subdivergent, puberulent, 10–53 mm long. Ovary cylindrical, 6–8 mm long, 2–3 mm thick, generally pubescent. Floral tube narrowly funnelform, 36–65 mm long, slightly bulbous at the base and 3–5 mm wide, narrowed to 2–4 mm wide above the nectary, then widened gradually above until (5–)6–10 mm wide at the rim, subglabrous to pilose or strigillose outside, pilose inside. Sepals narrowly lanceolate, 16–20 mm long, 3–7 mm wide, with mostly free, spreading tips in bud 1.5–2.5 mm long, divergent at anthesis. Tube and sepals bright scarlet. Petals orange red, oblong to lance-elliptic, 15–22 mm long, 4–7 mm wide, crispate-margined, often with a few, scattered hairs on the midvein dorsally, spreading-recurved at anthesis. Nectary light green, shallowly 4-lobed, 3–4 mm high, fused to the base of the tube in lower ⅔. Filaments red, 10–15 mm and 6–11 mm long; anthers narrowly oblong, 4–4.5 mm long, 1.5–2 mm wide, white. Style red, usually glabrous; stigma subobconic, 3–4 mm long, 2–3 mm wide, lightly 4-cleft apically, light red. Berry ellipsoid, 14–16 mm long, 8–10 mm thick, reddish; seeds tan, 1.1–1.4 mm long, 0.8–1.0 mm wide. Gametic chromosome number $n = 11$.

Distribution: Northern Peru. Locally frequent in thickets, frequently climbing up trees in forest openings, in mid-elevation cloud forest of Dept. Amazonas, east and northeast of Chachapoyas, 2,100–2,600 m; a few collections are also known from Dept. Cajamarca, Prov. Cutervo, 1,900–2,650 m (Fig. 60).

Representative specimens examined: PERU, AMAZONAS: 9 km E of Molinopampa on Chachapoyas-Mendoza road, *Berry & Escobar 3617* (MO, USM); Km 22 of Carretera Marginal E of Pedro Ruiz towards Rioja, *Berry & Escobar 3626* (MO, USM); on road to Pomacochas, 28 km above Puente Ingenio, *Hutchison & Wright 6778* (RSA, UC, USM); beyond Buenos Aires, Carretera Marginal, Dtto. Yambrasbamba, Prov. Bongará, *Tillett 673-213a* (VEN); Mendoza, *Woytkowski 8202* (MO); hills WNW of Pomacocha, *Wurdack 938* (F, NY, RSA, US). CAJAMARCA: Socata-San Andrés, *López & Sagástegui 5372* (MO); Achira, near Socota, Prov. Cutervo, *Velarde Nuñez 7065* (Z); El Suro, Prov. Cutervo, *Velarde Nuñez 7022* (Z).

This species is closely allied to *Fuchsia venusta* on the Northern Andes, which also has the unusual climbing habit, purplish stems, firm, nitid, short-petiolate leaves, and the axillary flowers with crispate-undulate petals. *Fuchsia rivularis* differs from that species in its generally quaternate leaves, less divergent pedicels, more numerous secondary veins, and spreading sepal tips in bud. Its distribution is centered in the moist cloud forests of central Dept. Amazonas, but three collections were seen from across the Río Marañón valley in Dept. Cajamarca that differ in their denser, short pilose pubescence, obtuse leaf tips, pilose styles, and slender floral tubes only 5 mm wide at the rim. Further habit and habitat information on these plants is necessary, however, before we can decide if these are distinct enough to warrant separate taxonomic recognition.

Fuchsia rivularis is sympatric with *F. pilosa,* but the two differ markedly in habit, and no hybrids have been detected.

30. Fuchsia gehrigeri Munz, Proc. Calif. Acad. Sci. IV. 25:41, *pl. 5, fig. 28.* 1943. TYPE: Venezuela, Edo. Mérida, Mucurubá, slopes and banks of La Cañada Grande, right fork of the town's stream, 2,800–3,100 m, 14 July 1930, *Wilhelm Gehriger 322* (US 1515306, holotype; F, G, GH, MO, NY, PH, VEN, isotypes).

Fuchsia jahnii Munz, Proc. Calif. Acad. Sci. IV. 25:40, *pl. 5, fig. 27.* 1943. TYPE: Venezuela, Edo. Mérida, Páramo de la Sal, 2,800 m, 2 Nov. 1921, *Alfredo Jahn 506* (US 1186509, holotype; photographs, NY, POM; GH, VEN, isotypes).

Erect to usually scandent-climbing shrubs 2–5 m high, with arching-pendant branches. Young growth sparsely puberulent to subcanescent, rarely densely pilose; branchlets subterete, subglabrous to strigose (rarely reddish pilose); older stems 8–18 mm thick, long and flexuous if climbing, with tan, flaky bark. Leaves mostly ternate, occasionally opposite or quaternate, membranous, (narrowly) elliptic to slightly (ob-)ovate, acute to obtuse or attenuate at the base, acute to subacuminate at the apex, 3.5–12 cm long, 1.5–5 cm wide, deep matte velvety green and strigillose to subglabrous above, pale dull green to purplish and strigillose below, hairs denser along the veins; secondary veins 5–12 on either side of the midvein; margin usually denticulate. Petioles light red, 10–40(–48) mm long. Stipules lanceolate, 1.5–2 mm long, divergent-spreading with age, subpersistent. Flowers axillary and clustered at the branch tips or sometimes corymbose with a rachis 2–6 cm long; flowers, pedicels, and flowering branches pendant. Pedicels loosely strigose, 12–40 mm long. Ovary ovoid, 5–7 mm long, 2–4 mm thick, strigillose to pilose. Floral tube narrowly funnelform, 40–50(–55) mm long, (2.5)3–4 mm wide and bulbous at the base, narrowed to 2–3 mm for the basal 18–22 mm of the tube, then gradually or usually abruptly widened and 8–9 mm wide near the rim, subglabrous to puberulent-strigose outside (rarely pilose), (densely) pilose or villous inside in lower 2–4 cm. Sepals lanceolate, acute to acuminate at the apex, (13–)15–21 mm long, (4–)5–6 mm wide, spreading at anthesis. Tube and sepals subnitid red. Petals scarlet, oblong to elliptic-obovate or lanceolate, 14–21 mm long, (4–)6–8 mm wide, obtuse to acute at the apex, margin and surface smooth, often with several hairs on dorsal surface, spreading to slightly recurved at anthesis. Nectary unlobed or slightly 4-lobed, 1.5–2 mm high. Filaments light red, sometimes whitish at the base, 10–14 mm and 8–12 mm long; anthers oblong,

2.5–3 mm long, ca. 1.5 mm wide, white. Style red, glabrous to loosely villous; stigma subglobose, 2–2.5 mm long, ca. 2 mm wide, slightly 4-cleft at the apex, dull cream to pink red. Berry ovoid to subglobose, somewhat quadrangular before maturity, 13–16 mm long, 10–13 mm thick, dark red purple at maturity; seeds 2–3 mm long, 1.1–1.4 mm wide. Gametic chromosome number $n = 11$.

Distribution: Venezuelan Andes and the Serranía de Perijá along the Colombian-Venezuelan border; in the Mérida Andes, in Trujillo, Mérida, and Táchira; in the Sierra de Perijá in Zulia, Venezuela and Cesar, Colombia, 2,200–2,800(–3,100) m, in cloud forest thickets and woods (Fig. 60).

Representative specimens examined: VENEZUELA, MÉRIDA: vicinity of Piñango, La Pinita, *Badillo 921* (VEN); between El Valle and Páramo La Culata, *Benítez de Rojas 1523* (MY); bridge of Quebrada El Valle, 7 km above Hotel Valle Grande, *Berry & Ruiz-Terán 2504* (MER, MERF, MO); Mucurubá, Quebrada El Rincón, above the town, *Berry & Ruiz-Terán 2509* (MER, MERF, MO); above Piñango, 4 km below Las Pailitas, 43 km W of Pico El Aguila, *Berry 3138* (MO, VEN); 9 km above Santo Domingo on road to Apartaderos, *Berry 3139* (MO, VEN), *3310* (MO), *3599* (MO); Mesa de Los Pinos, above La Mucuy, *Berry 3440* (MO, VEN), *3442* (MO), *3445* (MO, VEN); Páramo de Pinañgo, *Jahn 402* (US, VEN); Pueblo Llano, *López-Palacios 53* (MER); trail from La Escalera to Puente de la Escalera, *Luteyn et al. 6212* (MO); above Las Piedras, watershed of Río Aracay, *Ruiz-Terán et al. 8238* (MERF, MO); between El Arbolito and El Alto, N of Piñango, *Ruiz-Terán & Dugarte 12356* (MERF, MO); between El Chorrerón and La Cueva, road to Páramo de Palmita, *Ruiz-Terán & Dugarte 12489* (MERF, MO), *12493* (MO). TRUJILLO: above Jajó, *Aristeguieta & Medina 3397* (VEN); 12 km above and W of San Rafael on old Boconó-Trujillo road, *Berry 3098* (MO, VEN); ca. 3 km S of Las Mesitas, at Visún, Río La Coneja, *Berry 3128* (MO, VEN); 4–5 km along old Boconó-Trujillo road, 2 km S of lateral to Burbusay, *Tillett 739-573* (MO). ZULIA: Campamento Frontera II, near international boundary, headwaters of Río Negro, Sierra de Perijá, *Tillett & Hönig 746-678* (MO, VEN), *746-705* (MO, VEN), *746-766* (MO, VEN); Campamento Frontera V, on international boundary with Colombia, headwaters of Río Guasare, Sierra de Perijá, Serranía de Valledupar, *Tillett 746-1033* (MO, VEN), *746-1086* (MO, VEN). COLOMBIA, CESAR: Sierra de Perijá, E of Manaure, Sabana Rubia, *Cuatrecasas & Romero Castañedas 25061* (COL, RSA, US); Sierra de Perijá, E of Manaure, Quebrada de Floridablanca, *Cuatrecasas & Romero Castañedas 25224* (COL, US).

This species is characterized by its thin, denticulate, and rather long-petiolate leaves; its smooth, elliptic-oblong petals with frequent hairs on the back, and the ovoid-globose fruits with large seeds 2–3 mm long. It resembles *Fuchsia venusta* in its subracemose flowers, similar floral dimension, and frequent hairs on the petals. Since the two occur sympatrically, a list of their distinguishing characters is presented in Table 11. It may also be related to *F. petiolaris* from Colombia, which has similar leaves, large seeds, and pubescent petals.

Considerable leaf and pubescence variation occurs within a small area in different populations of *F. gehrigeri*. Characters such as differing pedicel lengths, hair length, and sepal tip length, however, which Munz used to distinguish *Fuchsia jahnii* from *F. gehrigeri,* were shown by field studies conducted near both type localities and in intermediate areas to be too variable to be of any taxonomic importance.

Plants that are unusually pilose, with smaller flowers than most populations of *F. gehrigeri,* are found above the town of Santo Domingo on the road to Apartaderos in Edo. Mérida. The hairs on these plants are often gland tipped and become reddish with age. A typical, less pubescent and longer-tubed plant of *F. gehrigeri, Ruiz-Terán et al. 8238* (MERF, MO) comes from a valley adjacent to Santo Domingo, however, indicating that the populations at Santo Domingo may be very localized variants.

Somewhat verrucose floral tubes and pedicels are found in populations north-

west of the city of Mérida, in the Valle Grande. These plants often have papillae protruding at the base of adjacent sepals. Some introgression may be occurring with *F. venusta,* because *Berry & Ruiz-Terán 2505* (MERF, MO; Quebrada Valle Grande, 7 km above Hotel Valle Grande) has morphological characters intermediate between the two species, such as smooth, elliptic petals of *F. gehrigeri* but subnitid, nearly entire leaves as in *F. venusta*. It has a pollen stainability of 66.8% (400 grains), compared to 94.7% (400 grains) for *Berry & Ruiz-Terán 2504* (MERF, MO), which is morphologically closer to *F. gehrigeri*. This valley has long been farmed and grazed by livestock, so these repeated disturbances may have led to an increased level of hybridization. In the same area, hybrids of *F. venusta* and *F. nigricans* are also found.

In contrast to El Valle Grande, populations of *F. gehrigeri* and *F. venusta* occur on virtually undisturbed slopes of primary cloud forest above La Mucuy, in the Parque Nacional Sierra Nevada, on the opposite side of the Río Chama from Mérida. There, a continual vegetation transect can be made following the trail from 2,250 m to 3,350 m at tree line (Fig. 6). *Berry 3439* (MO) was collected at 2,630 m and is apparently a hybrid between the lower elevational *F. venusta* and the mostly higher altitude *F. gehrigeri*. It has a low pollen stainability (31.5% of 400 grains) and the following intermediate morphological characters: subcoriaceous leaves, matte green above, but nitid below; petioles 8–20 mm long; and orange red flowers with smooth petals. *Bernardi 664* (NY; Edo. Mérida, Monte Zerpa, 2,600–2,800 m, June 1953) is another probable hybrid between *F. gehrigeri* and *F. venusta*. The floral tubes of this collection reach nearly 60 mm, and pollen stainability is 69% (1,000 grains examined).

An altitudinal separation similar to that of La Mucuy occurs further south in Edo. Táchira along the road from Zumbador to Queniquea. *Fuchsia venusta* is again the lower altitudinal species, occurring from 2,400–2,700 m on the eastern side of the ridge above Queniquea. *Berry 3295* (MO), *3296* (MO), and *3297* (MO, VEN; $n = 11$) occur at or just below the crest of the ridge, 4–6 km E of Zumbador, at 2,850–2,900 m, and resemble *F. gehrigeri* in their denticulate, long-petiolate leaves; the smooth, elliptic petals; and the ovoid-globose fruits with large seeds. The leaves tend to be broader and more ovate than the normal range of *F. gehrigeri,* however, and the sepals are strongly divergent, the branches ascending, and the floral tubes only gradually widened. Possible hybrids between these populations and *F. venusta* were collected on the east side of the ridge, 3 km E of Zumbador, at 2,760–2,775 m. *Berry 3414* (MO; $n = 11$) and *Luteyn et al. 5358* (NY) have unusually long floral tubes up to 78 mm long, elliptic, smooth petals, and subnitid, elliptic leaves with wine red stems. The floral tube length is greater than the extremes recorded in either *F. venusta* or *F. gehrigeri,* but the other characters are intermediate. Pollen stainability of *Berry 3414* is 69% (300 grains examined).

Fuchsia gehrigeri is also known to hybridize with *F. nigricans,* and the four putative hybrid collections are discussed under that species. It is also sympatric with *F. verrucosa,* but does not hybridize with that species.

A disjunct series of populations occurs in the Serranía de Perijá, along the Colombian-Venezuela border. The specimens from this area are very similar to those from the Mérida Andes except for the following differences: usually nar-

rower leaves with narrowly cuneate to attenuate bases, some petioles as long as 48 mm, more freely exfoliating bark, and generally more corymbose flowers. Petal shape varies in the few collections available from elliptic to lanceolate, but they are generally narrower, and the tips more acute, than plants from the main part of the range. None of the petals have dorsal hairs, however, which are usually found in populations from Mérida and Trujillo. More complete collections and additional field data from Perijá may in the future lead to the recognition of these populations as a separate taxon closely allied to *F. gehrigeri*.

31. Fuchsia llewelynii J. F. Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4):556. 1941. Munz, Proc. Calif. Acad. IV. 25:38, *pl. 5, fig. 25.* 1943. TYPE: Peru. Dept. Amazonas, La Ventana, path from Chachapoyas to Moyobamba, among shrubs on exposed rocky slopes, 2,700–3,300 m, 21 Jan. 1930, *Llewelyn Williams 7594* (F 626222, holotype; photographs, NY, UC).

Low shrubs with puberulent or canescent branchlets with spinescent projections, usually appearing papillose or verrucose when dry. Leaves opposite or ternate, membranous to subcoriaceous, narrowly oblong to elliptic or oblanceolate, acute at both ends, 2.5–9(–20) cm long, 1.2–4 cm wide, glabrous to strigillose on both surfaces; secondary veins 9–13(–25) on either side of the midvein; margin conspicuously dentate or serrulate. Petioles 3–9 mm long. Stipules narrowly lanceolate or filiform, 2–5 mm long, subpersistent. Flowers few and axillary at the branch tips or subracemose. Pedicels slender, puberulent, verrucose or with spinescent protuberances, 2–6 cm long. Ovary narrowly oblong, 5–6 mm long, ca. 1.5 mm thick. Floral tube cylindric-funnelform, (40–)45–54 mm long, slightly bulbous and 3–4 mm wide at the base, narrowed briefly to 2–3 mm wide above the nectary, then widened above until 5–8 mm wide at the rim, subglabrous to puberulent outside, pilose inside in lower ¾. Sepals narrowly lanceolate, acuminate, 13–17 mm long, 4–8 mm wide, with a tip ca. 2 mm long in bud. Tube and sepals dull pink. Petals pink, narrowly lanceolate to elliptic, acute to acuminate, 15–20 mm long, 4–8 mm wide. Nectary unlobed, ca. 2 mm high. Filaments 12–13 mm and 10–11 mm long; anthers oblong, 2.5–3 mm long, 1–1.5 mm wide. Style densely pilose for most its length; stigma subobconic, ca. 2 mm long, 1.5–2 mm wide. Berry ellipsoid, 12–15 mm long, ca. 8 mm thick.

Distribution: Northern Peru. Known from the mountains near La Ventana and Almirante, east of Chachapoyas and in the Serranía de Bagua, Dept. Amazonas, 2,600–3,300 m (Fig. 60).

Specimens examined: PERU, AMAZONAS: Cordillera Colán, SE of La Peca, Prov. Bagua, *Barbour 3828* (MO); Almirante, *Mathews 1480* (K, OXF); path between Chachapoyas and Moyobamba, *Weberbauer 4437* (G).

This species is apparently very rare and localized, as evidenced by the few specimens collected. The leaves are mostly narrowly oblanceolate and conspicuously toothed, but the most characteristic features are the long pedicels and unusual stems, which have numerous papillose or spinescent projections. The flowers are borne subracemosely, and the petals are slender and more or less recurved, characters that ally it to *F. venusta* and *F. rivularis*.

32. Fuchsia scherffiana André, Rev. Hort. 60:233, 268. 1888. TYPE: Ecuador, Prov. Zamora-Chinchipe, Alto Cruz Grande (4°32′S, 79°02′W), 19 Nov. (?) 1876, *Édouard André* (K, holotype). This is probably an H. Poortman collection, since he collected for André in southern Ecuador after André returned to Europe in Sept. 1876 (L. B. Smith, pers. comm.).

Erect to scandent shrubs 0.5–3 m tall with spreading branches. Branchlets canescent-strigillose, terete, 1–2.5 mm thick, purplish; older stems 3–10 mm thick, dull purple. Leaves opposite or occasionally ternate, firmly membranous, (very) narrowly elliptic to narrowly lanceolate, acute at the base, acute to acuminate at the apex, 2.5–10 cm long, 0.8–2.3 cm wide, (very) dark nitid green and strigose above, shiny green to metallic purple and strigose with long villous hairs along the midvein below; secondary veins 6–10 on either side of the midvein; margin subentire to slightly revolute. Petioles strigose, purplish, 4–15 mm long. Stipules lance-linear, dark, 1–2 mm long, ca. 0.3 mm wide, subpersistent. Flowers few and axillary, pendant. Pedicels strigillose, 15–20 mm long. Ovary oblong, strongly tetragonous, 7–8 mm long, 1.5–2 mm thick, greenish. Floral tube narrowly funnelform, 44–50 mm long, 2.5–4 mm wide and slightly bulbous at the base, narrowed to 2–2.5 mm wide above the nectary, gradually widened above until 7–8 mm wide at the rim, sparsely strigose outside, villous inside in lower ½. Sepals lanceolate, acuminate, 12–14 mm long, 3.5–5 mm wide, spreading at anthesis. Tube and sepals orange red. Petals red, narrowly elliptic-lanceolate, (narrowly) acute at the apex, 9–11 mm long, 3–5 mm wide. Nectary green, unlobed, ca. 1 mm high. Filaments red, 8–10 mm and 6–8 mm long; anthers oblong, 3–3.5 mm long, ca. 1.5 mm wide, cream. Style red, villous for ca. ¾ its length from the base; stigma globose, ca. 2 mm wide, 1.5–1.8 mm wide, reddish. Berry oblong, tetragonous, green before maturity, ca. 15 mm long, ca. 6 mm thick; mature fruits not seen.

Distribution: Southern Ecuador. Known only from the Nudo de Sabanilla area near the border of Loja and Zamora-Chinchipe Provinces, ca. 2,800 m (Fig. 60).

Specimens examined: ECUADOR, LOJA: road from Yangana to Nudo de Sabanilla, S of Yangana, 1 km below top of ridge, *Escobar 1547* (MO), *1547-A* (MO).

This is one of several localized, endemic species in southern Ecuador, including *Fuchsia steyermarkii* and *F. lehmannii*. It is characterized by its dark, metallic-colored, narrowly elliptic-lanceolate leaves, purplish stems, and long, axillary flowers with narrow petals. These characters place it closest to the *F. venusta* species group, and it is probably closely related to *F. llewelynii* of northern Peru. *Sandeman s.n.* (K; Aug. 1938) from Almirante, Dept. Amazonas in northern Peru possibly belongs in this species. It is somewhat less pubescent than the Ecuadorian plants, with less markedly angled ovaries and shorter pedicels, but agrees well in other floral and foliar characters with this species. Nearly mature fruits are present in this collection; the berries are ellipsoid, 13 mm long, and 7 mm thick. The seeds measure ca. 1.5 mm long and ca. 1 mm wide.

33. Fuchsia confertifolia Fielding & Gardner, Sert. Pl. *pl. 28*. 1844. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):550. 1941. Munz, Proc. Calif. Acad. Sci.

IV. 25:42, *pl. 6, fig. 30.* 1943. TYPE: Peru, Dept. Amazonas, Bagasán (on path from Molinopampa to Moyobamba), 1830–1841, *Andrew Mathews 1478* (OXF, holotype; photograph, MO; K, isotypes).

Fuchsia dolichantha K. Krause, Repert, Spec. Nov. Regni Veg. 1:172. 1905. TYPE: Peru, Dept. Amazonas, Tambo Ventilla, E of Chachapoyas, 2,400–2,600 m, 1904–1921, *August Weberbauer 4390* (B, holotype, destroyed in World War II; photograph, F).

Densely-branched shrubs 1–2.5 m tall. Branchlets terete, 1.5–3 mm thick, usually less than 15 cm long, conspicuously ferrugineous-hirsute; older branches with red brown bark exfoliating in slender strips. Leaves densely crowded on branchlets and upper portions of older stems with internodes mostly 2–5 mm long, 2–4 leaves per node, usually ternate, subcoriaceous, elliptic-ovate, rounded to acute at the base, acute at the apex, 8–12 mm long, 3–5 mm wide, glabrous on both sides except for scattered hairs 1.0–1.2 mm long on the basal portions of the midvein or along the margins; secondary veins 4–5 on either side of the midvein; margin remotely glandular-denticulate or slightly revolute. Petioles hirsute-villous, 1–2 mm long. Stipules dark, filiform, 2–3.5 mm long, ca. 0.3 mm wide, persistent, often connate and divergent to reflexed. Flowers mostly 2–8, drooping, grouped in uppermost axils at the branch tips. Pedicels hirsute, 9–15 mm long. Ovary oblong, 4–5 mm long, 1.5–2 mm thick, pilose, 8-sulcate. Floral tubes narrowly funnelform, 35–50 mm long, 2–4 mm wide and slightly bulbous at the base, narrowed to 1.5–3 mm wide above the nectary, gradually widened above until 7–10 mm wide at the rim, glabrous to sparsely pilose outside, pilose inside for most its length. Sepals narrowly lanceolate, acuminate, 13–18 mm long, 4–5 mm wide, with tips connate into a tip ca. 2 mm long in bud. Tube and sepals red. Petals red, narrowly triangular with long, tapered tips, 9–14 mm long, 2.5–3 mm wide, ⅓–¼ shorter than the sepals. Nectary unlobed, ca. 1.5 mm high. Filaments red, 6–10 mm and 4–7 mm long; anthers oblong, 2–2.5 mm long, ca. 1.5 mm wide. Style red, densely pilose for most its length; stigma subobconic, 4-cleft at the apex, 2–3 mm long, ca. 2 mm wide, exserted 4–5 mm beyond the anthers. Berry ellipsoid-ovoid, ca. 10 mm long, 5–7 mm thick; seeds tan, 1.8–2.1 mm long, 1–1.2 mm wide.

Distribution: Northern Peru. Endemic to cloud forest near high ridges of the mountains east of the Río Utcubamba in Dept. Amazonas, 2,600–3,200 m (Fig. 60).

Specimens examined: PERU, AMAZONAS: between Jumbilla and San Carlos, Prov. Bongará, *Weberbauer 7153* (F, GH, POM); S side of Molinopampa-Diosán Pass, N of Molinopampa, *Wurdack 1605* (F, NY, RSA, UC, US, USM).

This species is very distinctive in its densely crowded, small, leathery leaves and rust-colored hirsute stems. Its affinities are unclear, but it is placed in the *F. venusta* species group because of the coriaceous leaves, long, subracemose flowers, and somewhat ridged, delicate petals. It occupies the same restricted area as *F. pilosa*, *F. llewelynii*, and *F. wurdackii*, yet it is probably not sympatric with any of these species since it occurs at higher elevations.

34. Fuchsia denticulata Ruiz & Pavón, Fl. Peruv. Chil. 3:97, *pl. 325, fig. b.* 1802. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):553. 1941. Munz, Proc. Calif.

Acad. Sci. IV. 25:23, *pl. 2, fig. 9.* 1943. TYPE: Peru, "Cenchín, in cultis," probably Dept. Lima, 1778–1788, *Hipólito Ruiz & José Pavón* (MA N° 11/86, lectotype, here designated; photograph, MO). In the protologue, the locality is given as "Huassa-huassi et Cheuchín." The first site is in Junín, and the second apparently corresponds to the "Cenchín" on the lectotype label. Figs. 19, 42.

Fuchsia serratifolia Ruiz & Pavón, Fl. Peruv. Chil. 3:86, *pl. 325, fig. b.* 1802. Hook., Bot. Mag. *t. 4174.* 1845. Planch., Fl. Serres Jard. Eur. 5: *t. 447.* 1849. Sweet, Ornam. Fl. Gard. 2: *t. 88.* 1854. Essig, Nat. Hort. Mag. 13:12, *photo.* 1934. TYPE: Peru, Dept. Huánuco, Muña, 1778–1788, *Hipólito Ruiz & José Pavón* (MA, lectotype, here designated; photograph, MO).

Fuchsia leptopoda K. Krause, Repert. Spec. Nov. Regni Veg. 1:171. 1905. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):555. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:24, *pl. 2, fig. 10.* 1943. TYPE: Peru, Dept. Junín, Prov. Tarma, between Palca and Huacapistana, 2200–2600 m, 1904–1921, *August Weberbauer 1772* (B, holotype, destroyed in World War II; photographs, F, POM; G, isotype).

Fuchsia siphonata K. Krause, Repert. Spec. Nov. Regni Veg. 1:171. 1905. TYPE: Peru, Dept. Junín, Prov. Tarma, mountains E of Huacapistana, 1904–1921, *August Weberbauer 2178* (B, holotype, destroyed in World War II; photograph, F).

Fuchsia tacsoniiflora K. Krause, Repert. Spec. Nov. Regni Veg. 1:172. 1905. TYPE: Peru, Dept. Lima, near railroad from Lima to La Oroya, along streams above San Mateo, 3200 m, 1904–1921, *August Weberbauer 252* (B, holotype, destroyed in World War II; photograph, F).

Erect to scandent shrubs 1.5–4 m tall or climbing in trees to 10 m above ground. Young growth subcanescent or occasionally pilosulous; branchlets terete, subdivaricate, green to wine red; older branches 5–20 mm thick with tan, exfoliating bark. Leaves 3–5-verticillate, mostly ternate or quaternate, rarely opposite, firmly membranous, (narrowly) elliptic to oblanceolate, acute to narrowly cuneate at the base, acute to subacuminate at the apex, 4–17 cm long, 1.5–6.5 cm wide, dull to nitid dark green and glabrous above, pale green and subglabrous to strigose mostly along veins and margins below; secondary veins 7–17 on either side of the midvein, often reddish below; margin denticulate. Petioles glabrous to loosely strigose, (5–)8–20(–25) mm long. Stipules triangular, firm, often connate, 2–2.5 mm long, ca. 1.5 mm wide, deciduous. Flowers few to numerous, axillary and pendant, usually grouped toward branch tips. Pedicels stout, smooth, 1–1.5 mm thick, 18–45 mm long, suberect in bud, drooping at anthesis, generally green. Ovary narrowly oblong, terete, 10–13 mm long, 3–4.5 mm thick, generally glabrous, green. Floral tube subcylindric, firm, walls 1–1.5 mm thick, smooth, (28–)36–47 mm long, (3–)4–8 mm wide at the base, sometimes very slightly narrowed above the nectary, straight or slightly widened above until (5–)6–12 mm wide at the rim, glabrous to puberulent outside, densely villous inside above the nectary for 7–10 mm, glabrous above. Sepals lanceolate, acuminate, 17–26 mm long, 4–7 mm wide, forming a tapered point in bud, spreading to subdivergent at anthesis. Tube waxy light pink, lavender, or light red; sepals pink to light red with light green to whitish tips or margins, at times entirely whitish green. Petals orange to scarlet, usually drying purple streaked, lance-oblong to oblanceolate, obtuse to broadly acute at the apex, slightly undulate, 14–18 mm long, 4–6(–7) mm wide, suberect at anthesis. Nectary green, unlobed, 2.5–3 mm high, ca. 1.5 mm thick. Filaments pink to light red, 14–23 mm and 8–18 mm long; anthers oblong, 4–6 mm long, 2–3 mm wide, white. Style stout, pink to light red, glabrous; stigma subclavate, subentire (very slightly 4-cleft at the apex), 3–4 mm long, 2–3.5 mm wide, dull white, exserted 2–12 mm beyond the anthers. Berry ellipsoid,

20–26 mm long, 10–12 mm thick, nitid green to red purple, smooth surfaced; seeds tan, 1.8–2.2 mm long, ca. 1 mm wide. Gametic chromosome number $n = 11$.

Distribution: Peru and Bolivia. Known from three main areas: the Pacific slopes of the Cordillera Occidental of Peru in Lima and Ancash, near springs and in moist canyons, 2,800–3,500 m; on the eastern slopes of the Peruvian Andes from Huánuco to Cuzco, in cloud forest and moist upland shrub vegetation, 2,500–3,400 m; and on the northeastern slopes of the Bolivian Andes in Depts. La Paz and Cochabamba, in cloud forest, 2,200–3,100 m (Fig. 61).

Representative specimens examined: PERU, ANCASH: Racrán, near Chiquián, *Ferreyra 6208* (MO, US); Chiquián, *Ferreyra 7435* (F, MO, RSA, US); Km 23, Caraz, Prov. Huaylas, *López-Guillén 1904* (RSA); Caraz to Laguna de Parón, *López et al. 8348* (MO); above Monterrey, 3 km below Huaraz, *Pennell 15305* (PH). AYACUCHO: 41–47 km E of Tambo on road to Ayna, *Berry 3050* (MO, USM), *3052* (MO, USM); above Yuraccyacu on Capprichio-Puncu trail, ca. 40 km NE of Tambo, *Madison 10319-70* (MO, US, USM); above Jano, from Tambo to Ayna, *Plowman & Davis 4678* (GH, K); Yanamonte, between Tambo and Río Apurimac, *Weberbauer 5641* (F, GH, US); Choimacota valley, *Weberbauer 7587* (F, G, GH, S), *7587a* (F). CUZCO: Km 156–165 of Cuzco-Quillabamba road, Prov. La Convención, *Berry 2573* (CUZ, MO), *Berry & Aronson 3042* (MO, USM), *3043* (MO), *3048* (MO); Lucumayo valley, *Cook & Gilbert 1356* (US); Yuncaipata, Santa Rita, Prov. Convención, *Vargas 2656* (CUZ, MO); heights of Pintobamba, *Vargas 3551* (CUZ); Quellomayo-Lucumayo, *Vargas 4480* (BN, CUZ); Chawares, Prov. Convención, *Vargas 20237* (CUZ); above Alfamayo, *Vargas 22778* (MO). HUANCAVELICA: Salcabamba, Prov. Tayacaja, *Stork & Horton 10261* (F, UC); Montepungo, 5 km E of Surcubamba, Prov. Tayacaja, *Stork & Horton 10367* (F, G, NA, UC). HUÁNUCO: Carpish, *Ferreyra 1218* (MO, USM), *1730* (USM), *1832* (USM), *2088* (F, MO, NY, US, USM), *2387* (MO, US, USM); Mitobamba, above Mito, *Ferreyra 6683* (MO, US, USM); Carpish, above Acomayo, *Hutchison et al. 5921* (F, MO, NY, RSA, UC, US, USM); between Huánuco and Pampayacu, *Kanehira 236* (GH); Km 29–35 NW of Hacienda Mitobamba, Huánuco-La Unión road, *Luteyn & Lebrón-Luteyn 5501* (MO, NY); Muña, trail to Tambo de Vaca, *Macbride 4284* (F, GH, US); Mito, *Macbride & Featherstone 1403* (F, G, GH, US); ca. 23 km SE of Huánuco, *Macbride & Featherstone 2082* (F, GH, US); Muña, *Pearce 141* (K); Pillao, *Ruiz & Pavón 11/85* (F); Pampayacu, *Sawada P.8* (F); Pillao, *Woytkowski 34163a* (F, UC); Saraypampa, *Woytkowski 34194* (F, MO, UC). JUNÍN: 4 km W of Comas, road Concepción-Satipo, *Berry & Aronson 3065* (MO, USM); Comas, *Berry & Aronson 3066* (MO, USM); 69 km above and W of Satipo on road to Concepción, *Berry & Aronson 3072* (MO, USM); 62 km W of Satipo to Concepción, *Berry & Aronson 3076* (MO, USM); Palca, near Tarma, *Ferreyra 18738* (USM); Chilifruta, *Maguire & Maguire 61646* (NY); Pangoa, *Mathews 1168* (K); above Huacapistana, *Sandeman 4508* (K, OXF); Chaca, 5 km from Comas, *Vargas 22045* (CUZ). LIMA: Mani, near Huascoy, *Acleto 30* (MO, USM); between Infiernillo and Río Blanco, *Asplund 10846* (S, US); Llacshishi, Prov. Huarochiri, *Ferreyra 682* (MO, USM); near Palacala, above Surco, *Ferreyra 3415* (MICH, MO, US); between Huascoy and Cormo, *Ferreyra 18392* (MO); Infiernillo, *Goodspeed et al. 11549* (G, GH, NA, UC); Quebrada de San Mateo, *Isern 2546* (F); San Mateo, 1 km E of city, *Hutchison 669* (GH, UC, US, USM); Río Blanco, *Macbride & Featherstone 723* (F, GH); Huamatanga, *Mathews 541* (CGE, K, OXF); San Buenaventura, *Née s.n.* (MA 183589); Cerros de Matucana, *Raimondi 188* (USM). PASCO: Vitoc, *Martinet 1409* (P). WITHOUT LOCALITY: *Ruiz & Pavón s.n.* (BM, CGE, F, G, MA, MO). BOLIVIA, COCHABAMBA: ca. 42 km from Cochabamba to Chapare, *Berry 2584* (MO), *2585* (MO), *2586* (MO); near Chulumani on way to Yungas de Tablas, *Cárdenas 4087* (F, GH, RSA); Plumerito, to Río Tablas, *Cárdenas 6282* (US). LA PAZ: road to Chulumani, *Albert de Escobar 1305* (TEX); Yungas, *Bang 731* (F, GH, NY, PH, US); near Zongo, 32 km from crest of ridge, *Beck 2172a* (MO); Unduavi, *Brooke 6588* (BM, F, G, NY, U), *6850* (BM); *Buchtein 143* (F, G, GH, NY); Zongo valley, *Holliday 2/11* (K); San Felipe, Sur Yungas, *Holway & Holway 632* (US); Km 50 La Paz-Chulumani, *Kelley 1064* (BM, UC); near Combaya, Prov. Larecaja, *Mandon 623* (GH); Río Aceramarca, Cordillera Real, *Tate 718* (NY).

This is the most common and widespread member of the *Fuchsia denticulata* species group, an alliance of thick-tubed, axillary-flowered species centered in the Central Andes. It is characterized by its firm, subcylindrical flowers with waxy pink or light red floral tubes and narrow, green-tipped sepals, and also by the terete, ellipsoid fruits, stout pedicels, purple drying petals, large anthers 4–6 mm long, and nearly unlobed, clavate stigma.

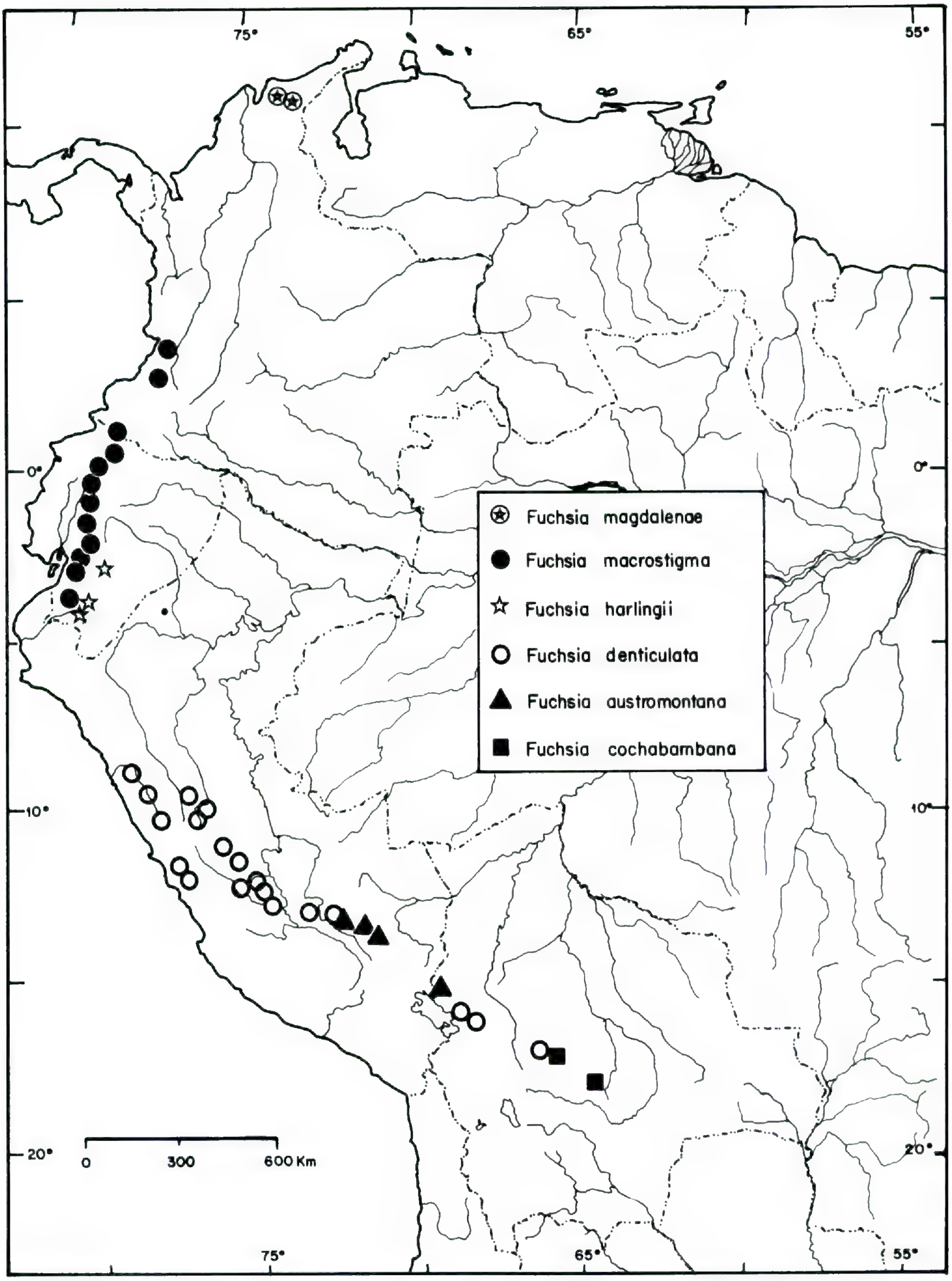


FIGURE 61. Distribution of the *Fuchsia denticulata* species group.

Fuchsia denticulata is the only member of the genus present on the dry Pacific slopes of the Cordillera Central in central Peru. It occurs there locally in isolated humid vegetation pockets, usually growing along streams, springs, or waterfalls. Plants from Ancash and Lima, such as the one used to describe *F. tacsoniiflora*,

TABLE 12. Comparison of diagnostic morphological characters of *Fuchsia denticulata*, *F. austromontana*, and intermediate Paucartambo collections.[1]

	F. denticulata	Paucartambo Collections[1]	*F. austromontana*
Leaf length	4–17 cm	5–13 cm	2.5–8 cm
Petiole length	(5–)8–20(–25) mm	7–12 mm	3–12 mm
Floral tube texture	Smooth	Tuberculate	Subtuberculate
Floral tube color	Pink to light red	Dark red	Dark red
Difference between widest and narrowest part of tube	2–3 mm	5–6 mm	4–6 mm
Sepal angle at anthesis	Spreading	Spreading-recurved	Spreading-divergent
Stigma color	Cream	Red pink	Red
Fruit transection	Terete	Terete (?)	Quadrangular

[1] See text for list of specimens.

generally appear more robust, with thicker stems than plants of this species growing on the eastern slopes of the Andes. This is probably due, however, to their upright, shrubby habit in the sparse vegetation of the Pacific slopes, compared to the typically scandent habit of *F. denticulata* in the dense thickets of cloud forests on the eastern slopes. This east-west disjunction of *F. denticulata* in the Peruvian Andes is discussed in greater detail on p. 26.

Plants with narrow leaves and floral tubes like the type of *F. leptopoda* appear sporadically throughout Junín and Ayacucho, but they intergrade completely with more typical populations and maintain characteristic traits of *F. denticulata* such as green sepal tips and purple-streaked petals when dry. In cloud forests along the eastern slopes of the Andes, *Fuchsia denticulata* can be found as an erect shrub, a scandent shrub, or a high climbing vine. This wide variability in habit type accounts for most of the variability found in leaf size, pubescence, and floral dimensions, which Krause and Ruiz and Pavón, used to describe several of the taxa included in the above synonymy.

There is a gap of some 500 km between the nearest collections from Peru and Bolivia. The related *F. austromontana* occurs in the intervening areas in southernmost Peru, at higher elevations than would be expected for *F. denticulata*. Populations intermediate in some characters between these two species occur between 1,900 and 2,500 m along the road from Paucartambo to Pilcopata, near Buenos Aires, in Dept. Cuzco, Peru. These include the following collections: *Berry et al. 2595* (MO, USM), *2598* (MO, USM; $n = 11$), *3007* (MO, USM); *Pennell 13970* (F, PH), *14047* (PH); *Vargas 10* (F); *Weberbauer 6934* (F, GH, US); and *West 7093* (GH, UC). These populations are sympatric with *F. tincta*, *F. vargasiana*, and *F. tuberosa* (sect. *Hemsleyella*), but occur several hundred meters lower than nearby populations of *F. austromontana* (Fig. 11). A comparison of these plants with *F. denticulata* and *F. austromontana* is presented in Table 12, showing their combination of distinctive and intermediate traits. Munz (1943) included some of the above specimens in *F. austromontana*; considering their ecological and morphological differences, however, this overextends the limits of that species. Further exploration in southern Peru (especially Dept. Puno) is needed to determine how widespread these variants are and if *F. denticulata* occurs in that area.

Fuchsia denticulata occurs sympatrically with *F. abrupta, F. corymbiflora, F. decussata, F. ferreyrae,* and *F. sanctae-rosae.* A Bolivian collection, *Beck 1266* (MO), is a probable hybrid with *F. sanctae-rosae* and is discussed under that species.

35. Fuchsia austromontana I. M. Johnston, J. Arnold Arbor. 20:242. 1939. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):548. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:22, *pl. 1, fig. 8.* 1943. TYPE: Peru, Dept. Cuzco, Prov. Paucartambo, between Pillahuata and Acanacu, 2,800 m, 26 July 1936, *James West 7083* (UC, holotype; photographs, NY, POM; GH, isotype).

Erect to occasionally climbing shrub 2–4 m tall. Young growth subcanescent to whitish pilose; branchlets subglabrous to puberulent, purplish, older branches with tan-brown, splitting bark. Leaves 3–5-verticillate, firmly membranous, acute to obtuse at the base, mostly acuminate at the apex, 2.5–8 cm long, 1–3 cm wide, dark green and subglabrous above, pale green and pubescent below, hairs usually denser along the midvein; secondary veins 5–9 on either side of the midvein; margin subentire to denticulate and sometimes slightly revolute. Petioles 3–12 mm long, reddish, densely pilose to lightly pubescent. Stipules linear-lanceolate, 2–4 mm long, 0.5–1 mm wide, subpersistent. Flowers generally few and pendant from upper leaf axils. Pedicels usually tuberculate, red, 14–35(–55) mm long. Ovary tetragonous, 6–8 mm long, 1.5–2 mm thick. Floral tube narrowly funnelform, walls ca. 1 mm thick, (25–)34–50 mm long, 4–6 mm wide at the base, then narrowed to 2–5 mm wide for lower ⅓, widened above until 10–12 mm wide at the rim, often ± verrucose, glabrous to densely pilose outside, (densely) villous inside in lower ⅓–¼. Sepals lanceolate, acute to acuminate, thick-spongy, ca. 1.5 mm thick when fresh, often verrucose, 15–20 mm long, 5–7 mm wide, spreading to divergent at anthesis. Tube and sepals scarlet, the tips sometimes dull purple green. Petals deep red, usually drying a uniform purple, elliptic-obovate to suborbicular, 12–17 mm long, (7–)8–13 mm wide, rounded to broadly acute at the apex, spreading at anthesis. Nectary deeply 4-lobed to unlobed, ca. 2 mm high. Filaments red, 10–14 mm and 7–10 mm long; anthers oblong, 3.5–4.5 mm long, 2–3 mm wide, white. Style red, glabrous or with a few hairs; stigma subglobose, 4-cleft at the apex, 2–2.5 mm long, ca. 3 mm wide, red pink, exserted 1–10 mm beyond the anthers. Berry ellipsoid, reddish, tetragonous before maturity, 16–18 mm long, 8–11 mm thick; seeds tan, 1.4–1.7 mm long, 0.8–1.1 mm wide. Gametic chromosome number $n = 11$.

Distribution: From southern Cuzco Dept. in Peru to just beyond the Bolivian border in Dept. La Paz, Bolivia; upper cloud forest shrubs, 2,600–3,500 m (Fig. 61).

Representative specimens examined: PERU, CUZCO: Acanaco, *Balls B6708* (BM, K, UC, US); Km 145 of Cuzco-Quillabamba road, *Berry 2568* (CUZ, MO); *3035* (MO, USM); 8 km E of Acanaco Pass, Km 101 of Cuzco-Pilcopata road, *Berry et al. 2594* (MO, USM); between town of Marcapata and the baños termales, *Berry & Aronson 3025* (MO, USM); Km 143–152 of Ollantaytambo-Alfamayo road, 58–67 km NW of Ollantaytambo, *Luteyn & Lebrón-Luteyn 6451* (MO); region of Acanacu and Cordillera de Tres Cruces, *Luteyn & Lebrón-Luteyn 6372* (NY); Pillahuata, Cerro de Cusilluyoc, *Pennell 14110* (F, GH, PH, US); Km 144 from Ollantaytambo to Chaullay, *Plowman & Davis 4749* (GH, K); Huaillai, Marcapata, *Vargas 1351* (BH, MO); between Achirani and Medias-Mayu, Prov. Paucartam-

bo, Dtto. Marcachea, *Vargas 11121* (F, UC). BOLIVIA, LA PAZ: Italaque, Prov. Camacho, *Cárdenas 3846* (LIL, POM).

This species is closely allied to *Fuchsia denticulata*, in a group of species with large, axillary flowers and thick floral tubes. *Fuchsia austromontana* grows at higher elevations than *F. denticulata* and has rounder, wider petals, tetragonous ovaries, and darker, somewhat verrucose flowers.

Fuchsia austromontana has a restricted range in southern Peru and just over the border into Bolivia. Populations that seem to intergrade with *F. denticulata* at intermediate elevations occur in Prov. Paucartambo, Dept. Cuzco, and are discussed under *F. denticulata* (Table 12 and Fig. 11). Another variant is *Metcalf 30548* (A, BH, F, G, MO, UC, US; Peru, Dept. Puno, Prov. Sandia, 9 km from Limbano at Chamacani, 2,700 m); it resembles *F. austromontana* except for its more acute, narrower petals (15 mm long, 6–7 mm wide), strongly spreading sepal tips, elongate ovaries, and dense pubescence. More collections of the *F. denticulata* species group are needed from southern Peru to better evaluate the pattern of variability in the species that occur there.

36. Fuchsia harlingii Munz, Aliso 7:409. 1972; Opera Bot., Ser. B, 3:16. 1974. TYPE: Ecuador, Prov. Loja, 14 km S of Saraguro, 3,000 m, 1–3 Aug. 1959, *Gunnar Harling 6192* (S, holotype; photograph, MO). Fig. 25.

Fuchsia fosbergii Munz, Aliso 7:409. 1972; Opera Bot., Ser. B, 3:15. 1974. TYPE: Ecuador, Prov. Loja, Cruz Loma, Cerro Villonaco, 6 km W of Loja, 2,980 m, 14 Feb. 1945, *Francis R. Fosberg & M. A. Giler 23036* (RSA 83773, holotype; US, isotype).

Erect to scandent shrubs 1–3 m tall. Branchlets subterete, 2–4 mm thick, glabrous or rarely strigose-villous; older branches with lustrous, purple brown bark, exfoliating in wide strips with age. Leaves opposite or ternate, firmly membranous to subcoriaceous, narrowly elliptic to elliptic-ovate, acute to rounded at the base, acute to acuminate at the apex, 3–7 mm long, 1.5–2.5 cm wide, glabrous and subnitid dark green above, pale green and glabrous to strigose-villous below; secondary veins 4–6(–7) on either side of the midvein, sometimes reddish below; margin glandular-serrulate. Petioles 3–6(–10) mm long. Stipules lance-deltoid, thick at the base, sometimes connate or recurved, 1–2 mm long, ca. 1.5 mm wide, subpersistent. Flowers few, pendant, and solitary in the upper leaf axils. Pedicels stout, 1–2 mm thick, 10–15 mm long. Ovary tetragonous, 6–7 mm long, 3–6 mm thick. Floral tube cylindric to narrowly funnelform, the base much wider than the ovary, (35–)44–53 mm long, very firm, 2–3 mm thick when fresh, (3–)4–9 mm wide at the base, 7–12 mm wide at the rim, gradually widened from the base to the rim or more often with subparallel sides, glabrous to villous outside, villous inside in lower ½. Sepals lance-oblong, 13–17(–21) mm long, 5–8 mm wide, 2–2.5 mm thick when fresh, spreading at anthesis, the tip blunt or less often acute in bud. Tube and sepals pale red to orange. Petals red, darker than the sepals, broadly elliptic-ovate, obtuse at the apex, 10–15 mm long, 7–11 mm wide, suberect at anthesis. Nectary shallowly 4–8-lobed, 1–2 mm high. Filaments red, 11–14 mm and 7–10 mm long; anthers oblong, 3–5 mm long, ca. 2 mm wide, cream. Style densely villous from the base to near the rim of the tube; stigma capitate, 4-cleft apically, 3–5 mm long, 3–5 mm wide, red. Mature berry not seen.

Distribution: Southern Ecuador, rare in cloud forest of Loja and Azuay Provinces, 2,600–3,300 m (Fig. 61).

Specimens examined: ECUADOR. AZUAY: Páramo and subpáramo N and NW of Páramo de Castillo, 6–8 km NNE of Sevilla de Oro, *Camp E-5184* (NY). LOJA: 10–12 km S of Saraguro, *Berry & Escobar 3193* (MO, QCA), *3195* (MO), *3206* (MO), *3207* (MO); Nudo de Guagrauma, S of Saraguro, *Correll E415* (LL); road from Loja to Saraguro, *Dodson & Thien 587* (DS); Cerro Arcana, *Espinosa & Williams 2490* (RSA); Km 51 on Panamerican Highway N of Loja, *Holm-Nielsen et al. 4701* (AAU, S); Saraguro, *Humboldt & Bonpland s.n.* (P); 12 km S of Saraguro, *King & Almeda 7840* (MO); Chuquirbamba, *Poortman 445* (P). SANTIAGO-MORONA or ZAMORA-CHINCHIPE: between Loma de Galapagos and headwaters of Rio Tintas, *Steyermark 53462* (NY). WITHOUT LOCALITY: *Lobb s.n.* (K).

This is a member of the thick-tubed, axillary-flowered *Fuchsia denticulata* species group and is distinctive in its firm, short petiolate, few-veined leaves, the short pedicels, and the smooth, purplish stems. Collections from the type locality near Saraguro, Loja, are usually glabrous with cylindric flowers that are broad at the base and blunt-tipped. Plants from other localities, however, have flowers narrower at the base with narrowly funnelform floral tubes and acute tips. This difference in tube shape was used by Munz (1972) to describe *F. fosbergii*; at that time Munz had seen only one other sheet of *F. harlingii*. *Berry & Escobar 3194* (MO), from near Saraguro, is densely hirsute, yet was collected from a population of totally glabrous plants. *Camp E-5184* (NY), the northernmost collection from Azuay, is also unusual in its strigose-villous pubescence.

Fuchsia harlingii is sympatric with the more widespread *F. loxensis*, but no hybrids between the two were detected.

37. **Fuchsia cochabambana** P. Berry, **sp. nov.** TYPE: Bolivia, Dept. Cochabamba, Prov. Chapare, Km 104 of Cochabamba-Villa Tunari road, 3,100 m, 18 Dec. 1966, *Roy F. Steinbach 632* (US 2533496, holotype; F, LAM, MO, NY, U, isotypes).

Frutex 0.5–1.5 m altus, ramulis foliisque glabratis vel puberulentis. Folia ternata vel interdum quaterna, subsessilia, elliptica vel anguste elliptico-lanceolata, basi acuta vel obtusa, apice acuminata, 3–12 cm longa, 1–5 cm lata, nervis secundariis utroque latere 11–14, margine valde denticulata vel serrulata; petiolis 1–3 mm longis; stipulis subpersistentibus, triangularibus, 2–3 mm longis, ca. 2 mm latis. Flores aurantiacorubri vel vivide coccinei, dependentes vel nutantes, axillares vel subracemosi ad apicem ramorum congesti; pedicellis 7–30 mm longis; ovario oblongo, 5–7 mm longo. Tubi florales anguste infundibuliformes, 45–58 mm longi, basi ca. 3 mm lati, superne sensim dilatati summo 7–10 mm lati. Sepala lanceolata acuminata 16–18 mm longa, ca. 5 mm lata. Petala rubra, in sicco saepe purpurascentia, elliptica, 10–13 mm longa, 5–8 mm lata, apice obtusa vel late acuta. Filamenta antisepala ca. 10 mm longa, antipetala 6–7 mm longa; antheris oblongis, ca. 3 mm longis, ca. 2 mm latis. Stylus ruber glaberque, stigmate rubro globoso apice leviter 4-fisso, ca. 3 mm longo, ca. 2 mm lato. Bacca matura non visa.

Shrubs 0.5–1.5 m tall. Young growth subglabrous to puberulent. Leaves ternate or less often quaternate, subsessile, firmly membranous, mostly elliptic or narrowly elliptic-lanceolate, acute to obtuse at the base, (sub-)acuminate at the apex, 3–12 cm long, 1–5 cm wide, subglabrous above, subglabrous to usually puberulent along the veins below and usually purple-flushed; secondary veins 11–14 on either side of the midvein; margin conspicuously dentate or serrate. Petioles 1–3 mm long. Stipules triangular, membranous when young to thick and recurved when old, 2–3 mm long, ca. 2 mm wide, subpersistent. Flowers pendant, few to numerous, axillary or subracemose, but always tightly grouped at the

branch tips. Pedicels 7–30 mm long. Ovary oblong, 5–7 mm long, ca. 2 mm thick. Floral tubes narrowly funnelform, 45–58 mm long, ca. 3 mm wide and slightly bulbous at the base, narrowed to ca. 2 mm wide above the nectary and gradually widened above until 7–10 mm wide at the rim, subglabrous to pubescent outside, pilose inside in lower ½. Sepals lanceolate, acuminate, 16–18 mm long, ca. 5 mm wide, with a narrow tip 2.5–3.5 mm long in bud. Tube and sepals orange red to bright crimson. Petals red, often drying purplish, elliptic, 10–13 mm long, 5–8 mm wide, obtuse to broadly acute at the apex. Nectary unlobed, ca. 2 mm high. Filaments light red, ca. 10 mm and 6–7 mm long; anthers oblong, ca. 3 mm long, ca. 2 mm wide. Style red, glabrous; stigma globose, 4-cleft apically, 2–3 mm long, ca. 2 mm wide, reddish. Mature berry not seen.

Distribution: Bolivia, scattered to locally frequent cloud forest shrubs in Depts. Cochabamba and Santa Cruz, 2,500–3,100 m (Fig. 61).

Specimens examined: BOLIVIA, COCHABAMBA: Cochabamba-Villa Tunari road, *Badcock 711* (K); Corani, *Cárdenas 5754* (K, US); Siberia, *Cárdenas 5764* (US). SANTA CRUZ: 24 km W of Comarapa on Carretera Fundamental 4, *Davidson 3851* (MO); Fortaleza, between Siberia and Comarapa, *Vogel 499* (U).

This species is included in the *Fuchsia denticulata* species group because of its long, firm floral tubes and purple drying petals. It differs from other members of this group in its funnelform floral tubes, nearly sessile, serrulate leaves, and flowers tightly grouped at the branch tips. This is one of only two species of sect. *Fuchsia* endemic to Bolivia, where it probably occurs sympatrically with *F. sanctae-rosae*.

38. Fuchsia macrostigma Bentham, Pl. Hartw. 129. 1844. *Fuchsia macrostigma* var. *typica* Munz, Proc. Calif. Acad. Sci. IV. 25:31, *pl. 3, fig. 17*. 1943. Based on *F. macrostigma* Benth. *Fuchsia macrostigma* var. *macrostigma*, Munz, Opera Bot., Ser. B, 3:19. 1974. TYPE: Ecuador, Prov. El Oro, in mountains of Paccha, 1841–1843, *Theodor Hartweg* (K, holotype; photograph, MO).

Fuchsia longiflora Bentham, Pl. Hartw. 177. 1845. *Fuchsia macrostigma* var. *longiflora* (Benth.) Munz, Proc. Calif. Acad. Sci. IV. 25:31. 1943; Opera Bot., Ser. B, 3:20. 1974. TYPE: Ecuador, Prov. Pichincha, W side of Volcán Pichincha, between Quito and Nanegal, 1841–1843, *Theodor Hartweg* (K, holotype).

Fuchsia spectabilis Hooker ex Lindley, Gard. Chron. 1848:319, *t.* May 13, 1848. Hook., Bot. Mag. 74: *t. 4375*. June 1, 1848. Lem., Fl. Serres Jard. Eur. 4:360, *t.* 1848. Paxt., Paxton's Mag. Bot. 16:255, *t.* 1849. Ysabeau, Journ. Hort. Prat. Belg. 7:225, *t.* 1849. Fancourt, Gard. Chron. 1850:71, *fig.* 1850. TYPE: cultivated in London, England, by the Veitch nurseries, 1848, from seeds collected by William Lobb in the mountains of Cuenca, Prov. Azuay, Ecuador, *William J. Hooker* (K, holotype).

Fuchsia macrostigma var. *pubens* I. M. Johnston, Contr. Gray Herb. 75:34. 1925. TYPE: Ecuador, Prov. Chimborazo, vicinity of Huigra, mostly on the Hacienda de Licay, 3 Sept. 1918, *Joseph N. Rose & George M. Rose 22479* (US 1022130, holotype; photographs, POM, UC; GH, NY, isotypes).

Erect shrubs 0.5–1.5 m tall. Branchlets stout, subsucculent, 2–7 mm thick, terete or angled, green to dull purple; older branches 8–15 mm thick, dull tan, with finely fissured bark. Leaves opposite or less often ternate, firmly membranous, narrowly to broadly elliptic to (ob-)ovate, acute at the base, acute to acuminate at the apex, 6–27 cm long, 3–12 cm wide, velvety dark green and subglabrous to puberulent above, pale green to wine purple below with strigose to

villous pubescence mostly along the veins; secondary veins 9–15(–22) on either side of the midvein; margin remotely denticulate with small, glandular teeth. Petioles stout, 2–3 mm thick, 15–30(–35) mm long, strigose, green to purple. Stipules dark, triangular, sometimes connate, 2–2.5 mm long, ca. 2 mm wide, deciduous. Flowers few and axillary in upper nodes. Pedicels stout, 2–2.5 mm thick, 8–20(–30) mm long, pubescent, spreading to ascending. Ovary cylindrical, 8–12 mm long, 3–5 mm thick, green, verrucose, 4–8 sulcate. Floral tubes narrowly funnelform, 50–80 mm long, 2–5 mm wide and bulbous at the base, gradually widened above until 4–10 mm wide at the rim, subglabrous to villous outside, sparsely pilose inside in lower ½; tube firm-spongy, 1–1.5 mm thick when fresh, often curved downward in distal ½. Sepals lance-oblong, 14–23 mm long, 7–8 mm wide, thick-spongy, 1–2 mm thick when fresh, apiculate, divergent, tips free and spreading in bud. Tube pale to dark red; sepals red with dull green tips. Petals bright red, shorter than the sepals, orbicular to broadly obovate, 12–18 mm long, 10–19 mm wide, undulate, rounded at the apex, strongly spreading. Nectary green, unlobed, ca. 3 mm high and ca. 1.5 mm thick. Filaments red, 8–12 mm and 5–8 mm long; anthers oblong, 2.5–3.5 mm long, ca. 1.5 mm wide. Style pink, sparsely pubescent to subglabrous; stigma massive, tetragonous, 3–5 mm long, 4–6 mm wide, with 4 mound-like, sticky lobes, cream to pink. Berry ellipsoid, 8-sulcate until fully ripe, verrucose, 20–22 mm long, 8–12 mm thick; seeds tan brown, 2–2.5 mm long, 1.2–1.6 mm wide.

Distribution: Cordillera Occidental of Colombia and Ecuador, infrequent in moist cloud forest thickets on Pacific slopes, 1,000–2,500 m (Fig. 61).

Representative specimens examined: COLOMBIA, CAUCA: Km 42–47 NE of Uribe, *Luteyn & Lebrón-Luteyn 7418* (COL, NY). NARIÑO: between Río Miraflores and Río San Martín, Volcán Cumbal region, *Ewan 16165* (POM, US); trail from Mayasquer to Tambo, *Vogel 284* (U). VALLE: above Queremal, Las Colonias, *Cuatrecasas 23901* (F). ECUADOR, AZUAY: W of Patul, 3 km between Huahualcay and Río Patul, below Pasas de Pinglión, *Steyermark 52613* (NY). BOLIVAR: Alto de Telimbela, *Acosta Solis 7156* (F); Simiatug, Hacienda Talahua, *Penland & Summers 614* (POM), *657* (F, POM). CAÑAR: N rim of valley of Río Cañar, *Camp E-2895* (NY, RSA). CARCHI: Km 50 Tulcán-Maldonado road, *Boeke 861* (MO); Km 71 on Tulcán Maldonado road, *Holm-Nielsen et al. 6011* (AAU); Los Olivos, *Mexia 7462* (F, NA, UC, US). CHIMBORAZO: Sibambe, Hacienda La Carmela, *Acosta Solis 5367* (F); 5 km from Huigra, Cañon del Río Chanchán, *Camp E-3376* (GH, MO, NY, P, RSA, UC, US); foot of Volcán Chimborazo, *Spruce in 1860* (K). COTOPAXI: 5 km above Pilaló, *Berry & Berry 2549* (MO); 3 km E of Macuchi, Quevedo-Latacunga road, *Dodson & Gentry 10152* (MO); Pilaló, *Holm-Nielsen & Jeppesen 1549* (AAU, DS). EL ORO: between La Chorita and Portovelo, *Hitchcock 21168* (GH, NY, US); along trail from Sambotambo, near highway to Portovelo, *Steyermark 54221* (NY). IMBABURA: Cerro de Pinam, *Acosta Solis 8505* (F); trail between Irubí and Apuela, N of Volcán Cotocachi, *Drew E-131* (RSA, US). PICHINCHA: valley of Río Pilatón, below Garretas, *Asplund 9709* (S); above Río Toachi, *López-Palacios 4224* (MERF, MO); Km 72–74 of old road Quito-Santo Domingo de los Colorados, *Luteyn & Lebrón-Luteyn 5651* (NY); 13 km NW of Nono, road to Puerto Quito, *Luteyn et al. 6520* (MO, NY); San Ignacio, Km 23 of Aloag-Santo Domingo road, *Sparre 14583* (S); Km 37–50 along Río Saloya, between Volcán Atacaso and Volcán Pichincha, *Steyermark 52543* (NY).

The flowers of this species are rather striking; they are long and narrow, usually horizontally disposed and recurved in the lower one half, with round, spreading petals, and a large, tetragonous stigma. Although it is a very distinctive species, it is placed in the *Fuchsia denticulata* species group because of its thick-tubed, axillary flowers, stout pedicels, and greenish sepal tips. The round petals, sulcate ovaries, and thick tubes also ally it to *F. ampliata,* however.

Fuchsia macrostigma is restricted to the Cordillera Occidental of the northern Andes and is the only species to be found in the southernmost remnant of cloud

forest in El Oro Province of southern Ecuador. Differences in floral tube length and degree of pubescence were used to describe the taxa listed in synonymy, but these characters vary too widely and continuously between populations to be of any taxonomic significance.

No naturally occurring hybrids of this species were found, but one of the earliest artificial hybrids in sect. *Fuchsia*, *F. dominiana* (van Houtte, 1854) was a cross between *F. macrostigma* and *F. denticulata*. *Fuchsia macrostigma* occurs sympatrically with *F. putumayensis*, *F. scabriuscula*, *F. sessilifolia*, and *F. sylvatica*.

39. Fuchsia magdalenae Munz, Proc. Calif. Acad. Sci. IV. 25:25, *pl. 2, fig. 5.* 1943. TYPE: Colombia, Dept. Magdalena, above San Miguel, at edge of páramo, 3,000 m, July 1932, *William E. Seifriz 392* (US 1572275, holotype; photographs, MO, NY, UC).

Fuchsia lampadaria J. O. Wright, Bot. Jour. Linn. Soc. 77:113, *fig.* 1978. TYPE: Cultivated in Reading, Great Britain in 1976, from seeds collected in Colombia, Dept. Magdalena, SE slopes of the Sierra Nevada de Santa Marta, Trombachuca Valley, uppermost forests, 3,300 m, 1975, by Michael Adams and George Bernard, *J. O. Wright* (RDG, holotype, not seen).

Shrubs 2–5 m tall. Young growth glabrous to lightly strigose; branchlets purplish, older branches red brown, with bark exfoliating in strips. Leaves ternate or less often quaternate, firmly membranous to subcoriaceous, (narrowly) elliptic to ovate, acute to rounded at the base, acute to subacuminate at the apex, 2.5–8.5(–12) cm long, 1–4(–6) cm wide, dark green and mostly glabrous above, pale green with purplish veins and glabrous below, except for hairs usually present along the margin; secondary veins 8–14 one either side of the midvein; margin denticulate or subentire. Petioles purplish, sparsely strigose, 4–25(–30) mm long. Stipules lanceolate to triangular, dark, ca. 1 mm long, deciduous. Flowers pendant and solitary in upper leaf axils. Pedicels firm, 15–60 mm long, mostly red. Ovary ovoid-ellipsoid, glabrous, 7–10(–11) mm long, 3–3.5 mm thick. Floral tube subcylindric, (35–)42–60 mm long, firm-fleshy, ca. 1 mm thick when fresh, 3.5–6 mm wide at the base, sometimes slightly narrowed above the nectary, very gradually widened above until 6–10 mm wide at the rim, glabrous inside and outside. Sepals lanceolate, acute to subacuminate, 13–18(–22) mm long, 4–5(–6) mm wide, blunt-tipped in bud, spreading at anthesis. Tube slightly purplish at the base and orange red above, sepals nitid orange red with greenish tips. Petals orange red, suborbicular to obovate or subrhomboid, sometimes with irregular margins, 11–19 mm long, 7–12(–18) mm wide, usually with a narrowly acute tip. Nectary an uneven band of lustrous tissue lining the basal 3–6 mm of the floral tube, without prominent lobes. Filaments light red, 12–16 mm and 8–13 mm long; anthers oblong, 3.5–4 mm long, ca. 2.5 mm wide, cream. Style light red to orange, glabrous; stigma capitate, lightly 4-cleft apically, 2–3 mm long, 2–4 mm wide, light red to orange, exserted 4–10 mm beyond the anthers. Berry ellipsoid, 20–24 mm long, 10–12 mm thick, usually dark purple; seeds (1.5–)2–2.5 mm long, 1–1.3 mm wide. Gametic chromosome number $n = 22$.

Distribution: Endemic to upper cloud forest of the Sierra Nevada de Santa Marta in northeastern Colombia; (2,000–)3,000–3,350 m (Fig. 61).

Representative specimens examined: COLOMBIA, MAGDALENA: SE slopes Sierra Nevada de Santa Marta, Dirincune Sabana, watershed of Río Donachui, *Cuatrecasas & Romero Castañeda 24514* (COL, RSA, US); San Antonio, Sierra Nevada de Santa Marta, *Hanbury-Tracy 504* (K), *518* (K); San Miguel, *Karsten s.n.* (W); Páramo in quebrada from Río Frío, ca. 10°55′N, 73°53′W, *Kirkbride & Forero 1759* (COL, MO); from Páramo to Cebolleta, *Romero Castañeda 7177* (COL); Pico Hacha-Sierra Nevada, *Schlim 800* (BM, F, G, K, MPU, P); between Pueblo and San Miguel, *Seifriz 537* (US).

This species is placed in the *Fuchsia denticulata* species group because of its thick-tubed, nearly cylindric, axillary flowers, but it is highly distinct from all other species in sect. *Fuchsia* in its non-annular, band type nectary, which resembles those found in sects. *Ellobium* and *Hemsleyella* (Figs. 45 and 48). Pubescence is completely lacking inside the tube and on the style, and the flowers have rounded petals that often have uneven margins. *Fuchsia magdalenae* is also tetraploid and has biporate pollen. The above assemblage of unusual characteristics suggests that this species may have been an early offshoot of the section that was isolated on an outlying portion of the Andes.

Fuchsia magdalenae is restricted to the upper cloud forest and subpáramo belt that more or less continuously surrounds the high peaks of the isolated Sierra Nevada de Santa Marta range. It is the only species of *Fuchsia* to occur there, although Wright (1978a) recently described *F. lampadaria* from this same area. Most of the differences he states for that species, however, are insignificant when all the specimens from the Santa Marta area are examined. The larger leaf dimension he describes may also be related to the controlled greenhouse conditions in which his plants were grown.

40. Fuchsia simplicicaulis Ruiz & Pavón, Fl. Peruv. Chil. 3:89. *pl. 322, fig. a.* 1802. Hook., Bot. Mag. *t. 5096.* 1859. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):563. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:41, *pl. 5, fig. 29.* 1943. Morley & Everard, Wild Flowers of the World, *pl. 173, fig. C1.* 1970. Travis, Fuchsia Annual 1975:21, *photo.* 1975. TYPE: Peru, Dept. Huánuco, woods at Muña, 1778–1788, *Hipólito Ruiz & José Pavón* (MA N° 11/92, lectotype, here designated; photograph, MO).

Scandent shrubs 2–5 m tall, sparsely verticillately branched, with ultimate branches pendulous. Branchlets subterete, puberulent, older stems with light red, exfoliating bark. Leaves ternate or quaternate, membranous, linear-lanceolate to ovate-lanceolate, acute to narrowly obtuse or truncate at the base, acuminate at the apex, 8–15 cm long, 1–3.5 cm wide, glabrous above, glabrous to scattered pilose below or along the margin; secondary veins 10–18 on either side of the midvein; margin subentire. Petioles glabrous to puberulent, 2–6 mm long. Stipules triangular, 1–2 mm long, ca. 0.9 mm wide, subpersistent. Flowers in simple to multiple, pendant, involucrate racemes, with flowers 3–4 per whorl and internodes 1.5–6 cm long; rachis 8–30 cm long; bracts thinly membranous, sessile, concave, ovate-lanceolate, broadly rounded and clasping the stem at the base, acuminate at the apex, 1–5 cm long, 0.5–1.5 cm wide. Pedicels puberulent, 5–10 mm long. Ovary oblong-ellipsoid, puberulent or velutinous, 5–6 mm long, 2–2.5 mm thick. Floral tube narrowly funnelform, 40–50 mm long, bulbous and 3–4 mm wide at the base, narrowed to 1.5–2 mm wide above the ovary, then gradually widened above until 5–7 mm wide at the rim, finely pilose outside, pilose inside.

Sepals lanceolate, puberulent on both sides, acuminate, 16–20 mm long, ca. 4 mm wide. Tube and sepals light reddish pink. Petals red, linear-lanceolate to elliptic, acute to narrowly acuminate at the apex, 9–13 mm long, 2–3(–5) mm wide. Nectary apparently unlobed, ca. 1.5 mm high. Filaments 10–12 mm and 7–8 mm long; anthers oblong, 3–4 mm long, ca. 2 mm wide. Style pilose from base up to the rim of the tube; stigma globose, 4-parted at the apex, 2.5–3.5 mm long, ca. 2 mm wide. Berry ellipsoid, puberulent, 11–13 mm long, ca. 8 mm thick; seeds tan, ca. 1.2 mm long, ca. 0.7 mm wide.

Distribution: Central Peru. Rare in cloud forests in Depts. Huánuco, Junín, and Pasco, eastern slopes of the Andes; 2,200–2,500 m (Fig. 62).

Specimens examined: PERU, HUÁNUCO: Muña, *Lobb 119* (K), *Macbride 4014* (BH, F, GH, K, S, US), *Pearce 133* (K). JUNÍN: Vitoc, *Martinet 1310* (P). PASCO: Oxapampa, *Soukup 1804* (GH, US, USM). WITHOUT LOCALITY: *Lobb s.n.* (K).

This is one of two very rare and unusual species with whorls or involucres of thin, membranous bracts and short-pedicelled flowers. The other species, *Fuchsia ceracea,* also occurs in Huánuco, but has much larger bracts and flowers, with shorter petals. Both species are glabrous except for the puberulent or velutinous young stems, pedicels, and flowers. Two other species from Central Peru, *F. coriacifolia* and *F. sanmartina,* seem to be derived from, or at least closely related to the above species. Their relationships are discussed further under the *F. simplicicaulis* species group (p. 54).

41. Fuchsia ceracea P. Berry, **sp. nov.** TYPE: Peru, Dept. Huánuco, Prov. Huánuco, in tree along stream, 5 km W of Carpish tunnel between Huánuco and Tingo María, 2,500 m, 4 Aug. 1978, *Paul E. Berry & James Aronson 3081* (MO 2720597, holotype; MO, USM, isotypes). Fig. 31.

Frutex scandens dependensque 3–6 m altus, praeter flores juvenes pedicellosque pilosos glaber. Folia opposita vel ternata, firme membranacea, lanceolata vel anguste ovata basi obtusa vel leviter auriculata aliquantum inaequalia, apice acuta, 8–15 cm longa, 4–6 cm lata, utrinque ceracea, nervis secundariis utroque latere 7–10, margine integerrima; petiolis leviter tortis 2–20 mm longis. Flores dependentes in verticillis involucratis 2–3 floralibus ad apicem ramorum disposisti; bracteis pruinosis, tenuiter membranaceis, concavis, sessilibus, late ovatis, 4–12 cm longis, 1.5–5 cm latis; pedicellis 7–15 mm longis; ovario ellipsoideo ca. 7 mm longo. Tubi florales vivide rosei vel lavandulacei, 9–13 cm longi, basi 6–7 mm lati inde 3–5 mm lati constricti superne gradatim dilatati summo 8–9 mm lati extus glabrati vel puberuli. Sepala lanceolata acuminata 28–30 mm longa 6–7 mm lata. Petala coccinea vel atropurpurea, ovata, late acuta, 5–7 mm longa, ca. 4 mm lata. Filamenta pallide rosea, antisepala 13–14 mm longa, antipetala 9–10 mm longa, antheris oblongis 4–5 mm longis ca. 3 mm latis. Stylus puberulus, stigmate magno subtetragono, 4-lobato, 4–5 mm longo ca. 4 mm lato. Bacca matura non visa. Numerus gameticus chromosomatum $n = 11$.

Climbing shrub or dangling liana in trees to 6 m above ground, the ultimate branches pendant. Plants glabrous except for puberulent young flowers and pedicels. Leaves opposite or ternate, firmly membranous, lanceolate to narrowly ovate, obtuse to unequal or slightly auriculate at the base, acuminate at the apex, 8–15 cm long, 4–6 cm wide, waxy green on both surfaces; secondary veins 7–10 on either side of the midvein; margin entire. Petioles reddish, slightly twisted, 2–20 mm long. Stipules narrowly triangular, 1.5–2 mm long, ca. 0.7 mm wide, subpersistent. Flowers in simple, pendant, involucrate racemes, with 2–3 flowers per whorl and internodes 2–6 cm long; bracts thin membranous, concave, sessile,

pruinose, broadly ovate, acuminate at the apex, clasping the stem at the base, 4–12 cm long, 1.5–5 cm wide. Pedicels 7–15 mm long. Ovary ellipsoid, ca. 7 mm long, ca. 3 mm thick. Floral tube subcylindric to narrowly funnelform, (9–)10–13 cm long, bulbous and 6–7 mm wide at the base, narrowed to 3–5 mm wide above the nectary, slightly widened above until 8–9 mm wide at the rim, puberulent to subglabrous outside, pubescent inside in lower ½. Sepals lanceolate, acuminate, 28–30 mm long, 6–7 mm wide, suberect at anthesis. Tube and sepals lavender to bright pink, tube white inside. Petals crimson to dark purple, ovate, broadly acute, 5–7 mm long, ca. 4 mm wide, suberect at anthesis. Nectary light green, unlobed, ca. 3 mm high. Filaments white pink, 13–14 mm and 9–10 mm long; anthers oblong, 4–5 mm long, ca. 3 mm wide. Style lavender pink, puberulent for most its length; stigma massive, subtetragonous, 4-lobed at the apex, 4–5 mm long, ca. 4 mm wide, light pink. Berry not seen. Gametic chromosome number $n = 11$.

Distribution: Very rare climbers in cloud forest, known just from Panao and the Carpish area of Dept. Huánuco, Peru; 2,500–2,850 m (Fig. 62).

Specimens examined: PERU, HUÁNUCO: above La Molina, near Panao, *Asplund 13699* (S); Carpish, *Asplund 14857* (RSA—a mixed collection with *F. corymbiflora*).

This species and *Fuchsia simplicicaulis* are the only two species in the genus with involucrate inflorescences and sessile concave bracts. *Fuchsia ceracea* has unusual waxy leaves, pruinose bracts, and very long floral tubes. The petals are less than one quarter as long as the sepals and are the proportionately most reduced of any species in sect. *Fuchsia*. It is extremely rare and is known only as a liana with long, unbranched, hanging stems. *Fuchsia abrupta* and *F. corymbiflora* both grow in the same area as *F. ceracea*, but they are lower shrubs and occur in more open thickets.

42. Fuchsia coracifolia P. Berry, **sp. nov.** TYPE: Peru, Dept. Pasco, Prov. Oxapampa, Huancabamba, 1863–1865, *Richard Pearce 565* (K, holotype; photograph, MO).

Frutex plerumque glaber 1–2 m altus. Folia coriacea subsessilia opposita vel ternata, basi rotundata vel subcordata apice acuta vel acuminata 3–6 cm longa 1–2.5 cm lata superne atroviridia subtus multo pallidioria, nervis strigulosis; nervis secundariis utroque latere 4–5 versus marginem gradatim inconspicuis; margine subdenticulata; petiolis 1–2 mm longis; stipulis plerumque connatis, subincrassatis, 2–3 mm longis, 2–3.5 mm latis, subpersistentibus. Flores rosei, numerosi et dependentes in racemo terminali et laxo dispositi, basi oppositi vel ternati apice gradatim alterni; rhachidi 3–9 cm longa; bracteis sessilibus anguste ovatis 10–20 mm longis 5–10 mm latis; pedicellis 5–15 mm longis; ovario oblongo 5–6 mm longo. Tubi florales firmi, anguste infundibuliformes, 52–58 mm longi, basi 3–3.5 mm lati et parum bulbosi inde 2.5–3 mm lati constricti superne gradatim dilatati summo 6–10 mm lati ubique plerumque glabrati. Sepala firma, ca. 1.5 mm crassa, oblongo-ovata, acuta, 17–19 mm longa 7–9 mm lata. Petala lanceolata acuta 10–12 mm longa ca. 4 mm lata. Filamenta antisepala 8–10 mm longa antipetala 6–7 mm longa, antheris oblongo-reniformibus 3–3.5 mm longis 2–2.5 mm latis. Stylus glaber, stigmate conico ca. 2 mm longo ca. 2.5 mm lato apice leviter 4-fisso. Bacca non visa.

Apparently simply branched low shrubs 1–2 m tall. Branchlets glabrous, slightly angled; older stems with whitish tan bark. Leaves opposite or ternate, firmly coriaceous, rounded to subcordate at the base, acute to acuminate at the apex, 3–6 cm long, 1–2.5 cm wide, dark green and strigillose along the veins above, much paler whitish green and strigillose along the red veins below; secondary

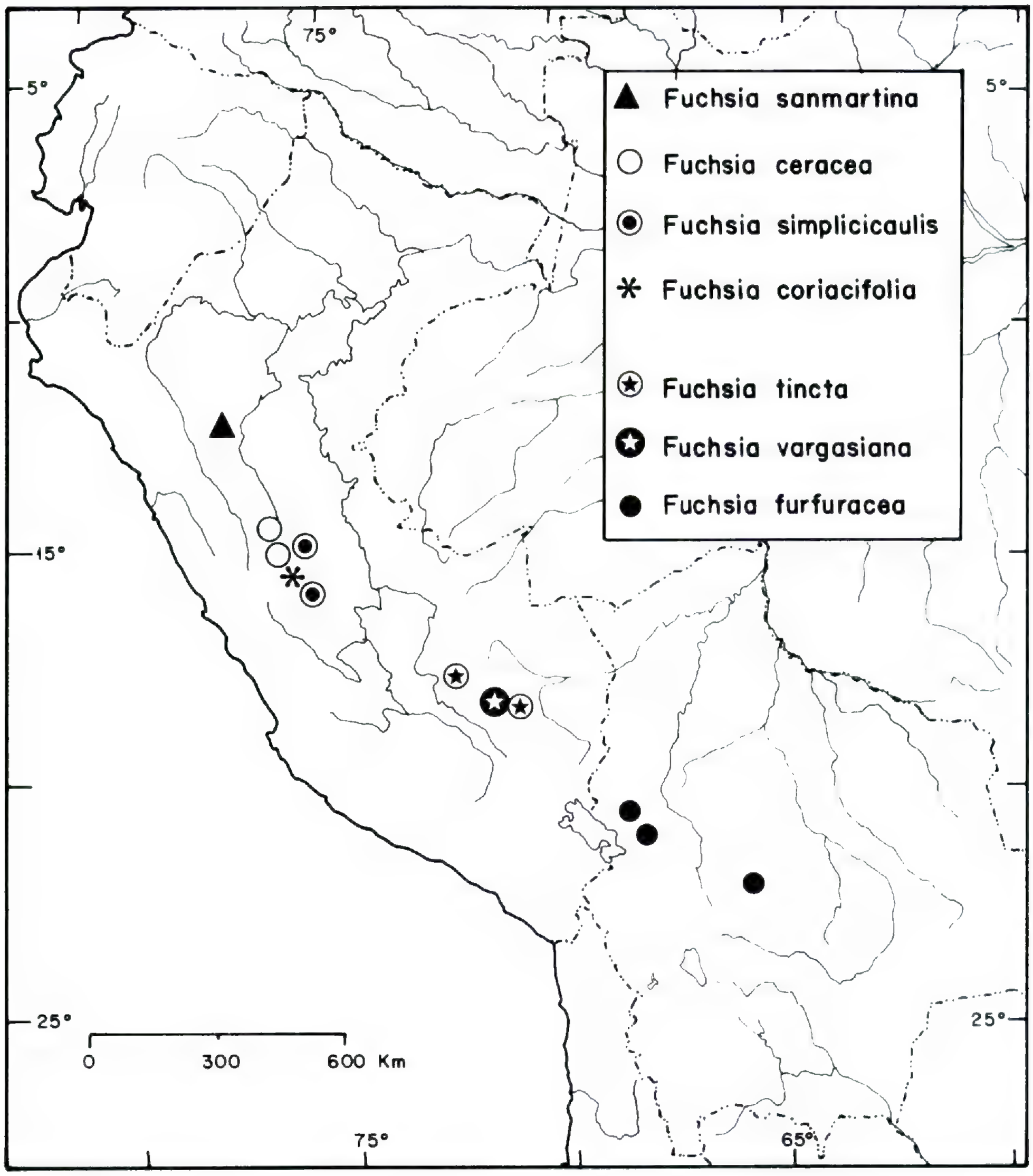


FIGURE 62. Distribution of the *Fuchsia simplicicaulis* and *F. tincta* species groups.

veins 4–5 on either side of the midvein, becoming inconspicuous towards the margin, the midvein prominent below; margin subdenticulate. Petioles 1–2 mm long, glabrous. Stipules mostly connate, firm, 2–3 mm long, 2–3.5 mm wide, subpersistent. Flowers numerous and pendant in loose, terminal racemes 3–9 cm long; bracts narrowly ovate, sessile, 10–20 mm long, 5–10 mm wide, opposite to ternate at the base and becoming alternate towards the end of the raceme. Pedicels 5–15 mm long, glabrous. Ovary ovoid, 5–6 mm long, ca. 3 mm thick. Floral tube narrowly funnelform, firm, 52–58 mm long, 3–3.5 mm wide and slightly bulbous at the base, narrowed to 2.5–3 mm above the nectary, then gradually widened above until 6–10 mm wide at the rim, mostly glabrous outside, glabrous inside. Sepals firm, ca. 1.5 mm thick, oblong-ovate, acute at the apex, 17–19 mm

long, 7–9 mm wide. Flowers rose. Petals lanceolate, acute at the apex, 11–12 mm long, ca. 4 mm wide. Nectary unlobed, 1.5–2 mm high. Filaments 8–10 mm and 6–7 mm long; anthers oblong-reniform, 3–3.5 mm long, 2–2.5 mm wide. Style glabrous; stigma conic, slightly 4-cleft at the apex, ca. 2 mm long, ca. 1.5 mm wide. Berry not seen.

Distribution: Known only from the type specimen, from central Peru, in Dept. Pasco near the Huánuco border (Fig. 62).

The ovate, sessile bracts, short pedicels, and inflorescence with opposite or ternate basal flowers place this species in the *Fuchsia simplicicaulis* species group. It is distinct from related species in having coriaceous, nearly sessile leaves and thick floral tubes. The inflorescence of *F. coriacifolia* seems to be derived from the involucrate type of *F. simplicicaulis* and *F. ceracea* and is transitional between these and the alternate-flowered, racemose inflorescences of the related *F. sanmartina*.

43. **Fuchsia sanmartina** P. Berry, **sp. nov.** TYPE: Peru, Dept. San Martín, Dist. Huallaga, Valley of Río Apisoncho, 30 km above Jucusbamba, 7°55′S, 77°10′W, 2,800 m, 6 Aug. 1965, *A. C. Hamilton & P. M. Holligan 1065* (K, holotype; photograph, MO; NY, S, UC, isotypes).

Frutex scandens 1.5–10 m altus, ramulis foliisque junioribus puberulenti-velutinis. Folia plerumque ternata interdum opposita, firme membranacea, anguste elliptico-ovata, basi obtusa vel rotundata aliquantum inaequalia apice acuta vel acuminata, 5–15 cm longa, 1.5–6 cm lata, subtus nervis plerumque puberulentis; nervis secundariis utroque latere 9–11, margine subintegerrima vel denticulata; petiolis puberulentis 3–20 mm longis; stipulis anguste triangularibus, ca. 2 mm longis, deciduis. Flores numerosi et dependentes, vivide rubri, racemis terminalibus dispositi; rhachidi 7–16 cm longa; bracteis 8–50 mm longis, 5–25 mm latis, petiolis 1–8 mm longis; ovario 7–8 mm longo. Tubi florales subcylindrici 55–76 mm longi basi 3–4 mm lati et parum bulbosi, inde 2–3 mm lati constricti superne gradatim dilatati summo 6–8 mm lato extus puberuli. Sepala lanceolata acuminata 20–25 mm longa 4–5 mm lata. Petala rubra anguste lanceolato-elliptica, acuta, 10–16 mm longa, 3–6 mm lata. Filamenta antisepala 14–15 mm longa antipetala 9–11 mm longa, antheris oblongis 3.5–4 mm longis 1.5–2 mm latis. Stylus pilosus, stigmate capitato, 3–4 mm longo, 2.5–3 mm lato apice leviter 4-fisso. Bacca matura non visa.

Scandent shrubs 1.5–3 m high or lianas to 10 m above ground. Young growth finely puberulent-velutinous, branchlets mostly subtriangular in transection. Leaves mostly ternate, occasionally opposite, firmly membranous, narrowly elliptic-ovate, obtuse to rounded or unequal at the base, acute to acuminate at the apex, 5–15 cm long, 1.5–6 cm wide, subglabrous to puberulent above, puberulent below, especially along the veins; secondary veins 9–11 on either side of the midvein; margin subentire to denticulate. Petioles puberulent, 3–20 mm long. Stipules narrowly triangular, ca. 2 mm long, deciduous. Flowers numerous and pendant in terminal racemes; rachis puberulent, 7–16 cm long; bracts 8–50 mm long, 5–25 mm wide, with petioles 1–8 mm long. Pedicels puberulent, 13–50 mm long. Ovary oblong, 7–8 mm long, ca. 2 mm thick. Floral tube subcylindric, 55–76 mm long, bulbous and 3–4 mm wide at the base, then narrowed to 2–3 mm wide above the nectary, slightly widened above until 6–8 mm wide at the rim, puberulent outside, pilose inside. Sepals lanceolate, acuminate, 20–25 mm long, 4–5 mm wide, the tips slightly spreading in bud. Tube and sepals bright red. Petals red, narrowly lance-elliptic, acute, 10–16 mm long, 3–6 mm wide. Nectary unlobed, ca. 2 mm high. Filaments 14–15 mm and 9–11 mm long; anthers oblong, 3.5–4 mm long,

1.5–2 mm wide. Style pilose, stigma 3–4 mm long and 2.5–3 mm wide, 4-parted at the apex. Berry not seen.

Distribution: Known only from the type locality and near vicinity on the eastern slopes of Dept. San Martín, Peru; 2,800–3,600 (Fig. 62).

Specimens examined: PERU, SAN MARTÍN: Valley of Río Apisoncho, 30 km above Jucusbamba, 3,600 m, *Hamilton & Holligan 336* (K, S, UC).

This species belongs to the *Fuchsia simplicicaulis* species group because of its narrowly elliptic-ovate leaves, nearly sessile bracts, and terminally grouped, finely puberulent flowers with petals much shorter than the sepals. It lacks the unusual sessile, concave bracts and involucrate flowers of *F. simplicicaulis* and *F. ceracea,* but it is linked to these species by *F. coriacifolia,* which has an intermediate type of inflorescence, with the older flowers verticillate and the younger flowers alternate.

Hamilton & Holligan 1157 (K), from the type locality, differs from the previously cited specimens of this species in its longer, redder pubescence, shorter petals (6–8 mm long), and much more spreading sepal tips. There are presently too few specimens available to know if this collection falls within the normal variability of *F. sanmartina*.

44. Fuchsia sessilifolia Bentham, Pl. Hartw. 176. 1845. Hook., Bot. Mag. *t. 5907.* 1871. Munz, Proc. Calif. Acad. Sci. IV. 25:67, *pl. 11, fig. 57.* 1943; Opera. Bot., Ser. B, 3:22. 1974. TYPE: Ecuador, Prov. Pichincha, woods of Guayán, W slopes of Volcán Pichincha, 1841–1843, *Theodor Hartweg 985* (K Bentham Herb., holotype; photograph, MO; BM, BREM, CGE, K Hooker Herb., OXF, isotypes).

Erect to scandent shrubs 0.5–3 m tall with few, erect to mostly arcuate branches. Young growth finely puberulent, branchlets subtetragonous, cinereous-puberulent, 2–6 mm thick, wine red; older branches 5–15 mm thick, with exfoliating bark. Leaves verticillate, mostly quaternate, subsessile, membranous to subcoriaceous, narrowly elliptic to elliptic or oblanceolate, rounded to attenuate or narrowly subcordate at the base, acute to acuminate at the apex, 6–20 cm long, 2–6(–8) cm wide, lustrous dark green and subglabrous above, pale green to purplish and pubescent to subglabrous below; secondary veins 18–25 on either side of the midvein, impressed above, the midvein prominent below; margin serrulate and commonly undulate. Petioles 1–5 mm long, dull red. Stipules triangular, thickened at the base, 1–2 mm long, ca. 1 mm wide, mostly deciduous. Flowers numerous in terminal, drooping, verticillately-branched panicles; rachis 5–30 cm long, bracts lanceolate, 10–35 mm long, 4–10 mm wide, often reflexed. Pedicels slender, strigillose, 3–5(–8) mm long. Ovary cylindrical, 5–6 mm long, 1.5–2.5 mm thick, finely strigose. Floral tube narrowly funnelform, 13–18(–20) mm long, 2–3 mm wide at the base, narrowed slightly to 1–2 mm above the nectary, gradually widened above until 4–5 mm wide at the rim, finely strigose outside, pilose inside. Sepals lanceolate, 8–11 mm long, 3–4 mm wide, acute to acuminate, forming a short point 1–2 mm long in bud, spreading at anthesis. Tube pale cream to rose green or light red; sepals light yellow green to light pink. Petals bright scarlet,

contrasting with the lighter sepals and tube, elliptic-oblanceolate, 6–9 mm long, 3–4 mm wide in the middle, acute to rounded at the apex, spreading at anthesis. Nectary unlobed, ca. 1 mm high. Filaments red to greenish red, 5–8 mm and 3.5–5 mm long; anthers oblong, 1.5–2 mm long, ca. 1 mm wide, pale yellow. Style glabrous to loosely pilose; stigma capitate, 4-parted at the apex, 1.5–2 mm long, 1.5–2 mm wide, cream, situated at the level of the anthers or slightly exserted. Berry cylindric-oblong, 15–19 mm long, 8–11 mm thick, green to nitid purple; seeds reddish purple to tan, 1.5–2 mm long, ca. 1 mm wide. Gametic chromosome number $n = 11$.

Distribution: Ecuador and Colombia. In the Cordillera Occidental of the Northern Andes from Pichincha, Ecuador to Chocó and Antioquia, Colombia; in the Cordillera Central from northern Napo to Tolima; and in the Cordillera Oriental from Putumayo to Huila; cloud forest shrubs in thickets, streambanks, and forest openings; 2,300–3,200 m (Fig. 63).

Representative specimens examined: COLOMBIA, ANTIOQUIA: without locality, *Kalbreyer in 1879* (K). CAQUETÁ: Pass between Garzón and Florencia, *Mason 13930* (COL, GH, UC, US). CAUCA: above Carpintería, *Alston 8232* (BM, COL, RSA, S, US); between Guachicono and Río Putis, *Core 936* (MICH, RSA, US); Finca La Cumbre, headwaters of Río Dinde, *Core 1086a* (US); Quebrada de Santo Domingo, headwaters of Río Palo, Cordillera Central, *Cuatrecasas 19297* (A, F, NY, VALLE); Aguabonita, region of Moscopán, east slopes Cordillera Central, *Cuatrecasas 23555* (F, RSA); Vinagrita tibia, Puracé, *Dryander 1633* (US); west slopes of Río Munchique, *García-Barriga et al. 12928* (AAU, COL, US); W of Tambo, Cordillera Occidental, *Haught 5191* (COL, P, RSA, US); Páramo de Las Papas, between El Boquerón and La Hoyola, *Idrobo et al. 3919* (COL, P); Volcán de Sotará, *Lehmann 6220* (K); Canaan, Puracé, *Pennell & Killip 6674* (GH, NY, PH, US); Paletara to Calaguala, *Pennell 7111* (GH, NY, PH, US); San José, San Antonio, *Pennell 7569* (GH, NY, PH, US); above Carpinterías, between Cerros Munchique and Altamira, *Pérez-Arbelaez & Cuatrecasas 6145* (COL, F, US); valle de Quintero, near Pitaió, Río Palo basin, *Pittier 1427* (NY); road from Tambo to 20 de julio, *Plowman & Vaughan 5315* (COL). CHOCÓ: headwaters of Río Carmen, 8 km N of Carmen de Atrato, *Fosberg 21560* (RSA, US); Dauro, *Toro 1168* (NY). HUILA: Km 25 of Pitalito-Mocoa road, *Berry 3592* (COL, MO); between Gabinete and Andalucía, *Cuatrecasas 8586* (COL, F, US); Finca Merenberg, Municipio de La Playa, *Díaz Piedrahita et al. 405* (COL); Lavaderos, ridge between Ríos Naranjo and Granadillo, 15 km S of San Agustín, *Fosberg 20062* (RSA, UC, US); 20 km from Altamira toward Florencia, *Luteyn et al. 4846* (COL, MO); between Garzón and Florencia, *Mason 13921* (UC); E of Neiva, *Rusby & Pennell 687* (NY, US). NARIÑO: above El Encano, Laguna La Cocha, *Balls 7521* (BM, COL, K, NA, UC, US); between Pasto and Río Bobo, *Barclay 4670* (COL, MO); Gruta de la Virgen, road Pasto to Yacuanquer, *Benavides 31* (PSO); Aponte, Río Majinsanoy, *Bristol 1177* (COL, DS); right bank of Río Barrancos, Municipio de La Florida, *Díaz et al. 831* (COL); Encano, N end of Laguna La Cocha, *Fosberg 20431* (RSA, S, US); Laguna La Cocha, Isla La Corota and Sixce-Turibamba, *García-Barriga et al. 13049* (COL, US); woods near Pasto, *Jameson 432* (BM, CGE, G, K, LE, OXF, TCD); road from Cuatro Esquinas to Quitasol, *Mora 293* (COL); road from Balalaika to Yascual, *Mora 396* (COL); near crossroads of El Pedgregal-Ipiales road, Guacuán path, *Mora et al. 6056* (PSO). PUTUMAYO: 2 km SW of Sibundoy, *Bristol 328* (COL, DS, GH); Km 79 from Pasto to San Francisco and Mocoa, *Plowman & Davis 4315* (COL); Páramo de San Antonio, road Pasto-Sibundoy, *Schultes & Cabrera 18883* (US); near Sibundoy, *Schultes & Smith 3061* (BH, DS, MO, NY, UC). QUINDÍO: 12 km from Salento towards Cocora, along Río Salento, *Escobar 1014* (MO). TOLIMA: Buenavista, *André 2134* (F, GH, K, NY): Quindío, *Triana s.n.* (G 2 sheets, P); Mt. Quindío before El Gallego, *Triana 6125.6* (BM, COL). VALLE: Barragán, watershed of Río Bugalagrande, La Laguna, *Cuatrecasas 20863* (F, RSA, VALLE); La Palma, right bank Río Pichindé, watershed of Río Cali, *Cuatrecasas 21672* (F, RSA, VALLE); Río Cali, Pichindé, *Duque-Jaramillo 4702* (COL); near Palmira, near Quebrada El Socorro, Cordillera Central, *Maas & Escobar 628* (MO, U). ECUADOR, CARCHI: Km 57 of Tulcán-Maldonado road, *Boeke 828* (MO); 5 km W of El Carmelo, *Berry 3163* (MO, QCA); El Pun (= El Carmelo), *Asplund 16890* (K, NY, S), *Mexia 7579* (POM, RSA, UC, US). IMBABURA: Urcusique, W slopes of Volcán Cotacachi, *Acosta Solis 8225* (F). NAPO: Santa Bárbara de Sucumbios, along Colombia border, *Harling 4130* (NY, S); Río San Pedro below mouth of Río Clavadero, E of Cayambe peak, *Wiggins 10454* (DS). PICHINCHA: Guarumal, Km 38 of road to Saloya, *Acosta Solis 11008* (F); Saloya, W of Quito, *Asplund 7302* (S); Chiriboga, *Asplund 17146*

(NY, S); near Atahualpa, *Asplund 20314* (NY, S); above Chaupi-Saycha, Pululagua, *Bell 513* (BM); above San José de Minas, *Benoist 3963* (F); 41 km W of Cotocollao to Nanegal, *Berry & Escobar 3182* (MO, QCA); 34 km W of Chillogallo to Chiriboga, *Berry & Escobar 3242* (MO, QCA); Cornejo Astorga, road Quito-Santo Domingo de los Colorados, *Harling et al. 9355* (MO, RSA); below Nono, *Haught 3166* (A, BH, US); above Tandapi, *Holm-Nielsen et al. 7130* (AAU); Alaspongo, *Holmgren & Heilborn 697* (S); Mt. Corazón and Lloa, *Sodiro s.n.* (W); San Ignacio, road Aloag-Santo Domingo, *Sparre 14596* (S); Km 37–50 along Río Saloya, between Volcanes Atasco and Pichincha, *Steyermark 52513* (NY).

This is an easily recognizable species due to its large, lanceolate, subsessile, and quaternate leaves and the terminal, drooping panicles of short, pale flowers with contrasting dark petals. It is one of the most widespread species in the genus, occurring in Ecuador on both sides of the Andes and in all three cordilleras of the northern Andes. Its distribution pattern indicates a probable origin in the Cordillera Occidental of Ecuador with a subsequent northward extension into the southern parts of the Colombian cordilleras. As a result of this wide distribution, it is sympatric with many taxa of *Fuchsia*, including *F. cuatrecasasii, F. corollata, F. dependens, F. hartwegii, F. nigricans, F. scabriuscula, F. sylvatica, F. polyantha*, and *F. verrucosa*. It is only known to hybridize with *F. nigricans* (see discussion under that species).

Fuchsia sessilifolia has flowers similar to *F. nigricans* in the contrasting petal and tube colors, short tubes, and cylindrical ovaries, but it has a much more branched inflorescence. It is very closely allied to *F. polyantha*, which can only be distinguished by its longer, totally red flowers. The two species occur together or in close proximity on the western slopes of the Ecuadorian Andes, and their different floral tube lengths and flower coloration may be related to different pollinators, or to the development of mechanical factors that reduce the chance of interspecific pollination.

45. Fuchsia polyantha Killip ex Munz, Proc. Calif. Acad. Sci. IV. 25:48, *pl. 7, fig. 37*. 1943. Munz, Opera Bot., Ser. B, 3:21. 1974. TYPE: Colombia, Dept. Nariño, between Mayasquer and Tambo, 2,800 m, 2 Aug. 1935, *Ynes Mexia 7571* (US 1662416, holotype; photographs, NY, POM; F, UC, US, isotypes).

Erect shrubs 1–2 m tall. Young growth minutely puberulent-canescent; branchlets puberulent, terete, purplish. Leaves quaternate, firmly membranous, narrowly elliptic-lanceolate, acute to obtuse at the base, acuminate at the apex, 7–12 cm long, 2.5–4 cm wide, nitid dark green and subglabrous above, light green and sparsely puberulent below, especially along the veins; secondary veins 13–16 on either side of the midvein; margin subentire to serrate. Petioles puberulent, purplish, 3–10 mm long. Stipules dark, thick at the base, triangular, 1.5–2 mm long, ca. 1 mm wide, often connate and recurved when old, persistent. Flowers numerous in terminal, nodding, verticillately branched panicles; rachis 8–15 cm long; bracts narrowly lance-ovate, recurved, 10–30 mm long, 5–10 mm wide. Pedicels puberulent, 5–10 mm long. Ovary fusiform, puberulent, 6–7 mm long, ca. 2 mm thick. Floral tube narrowly funnelform, 34–43 mm long, slightly nodose and 2.5–3.5 mm wide at the base, narrowed to ca. 2 mm above the nectary, then widened above until 5–7 mm wide at the rim, finely puberulent outside, pilose inside in lower ½. Sepals narrowly lanceolate, acuminate, 10–15 mm long, ca. 3 mm wide, with a narrow tip 1.5–2 mm long in bud. Tube and sepals red. Petals

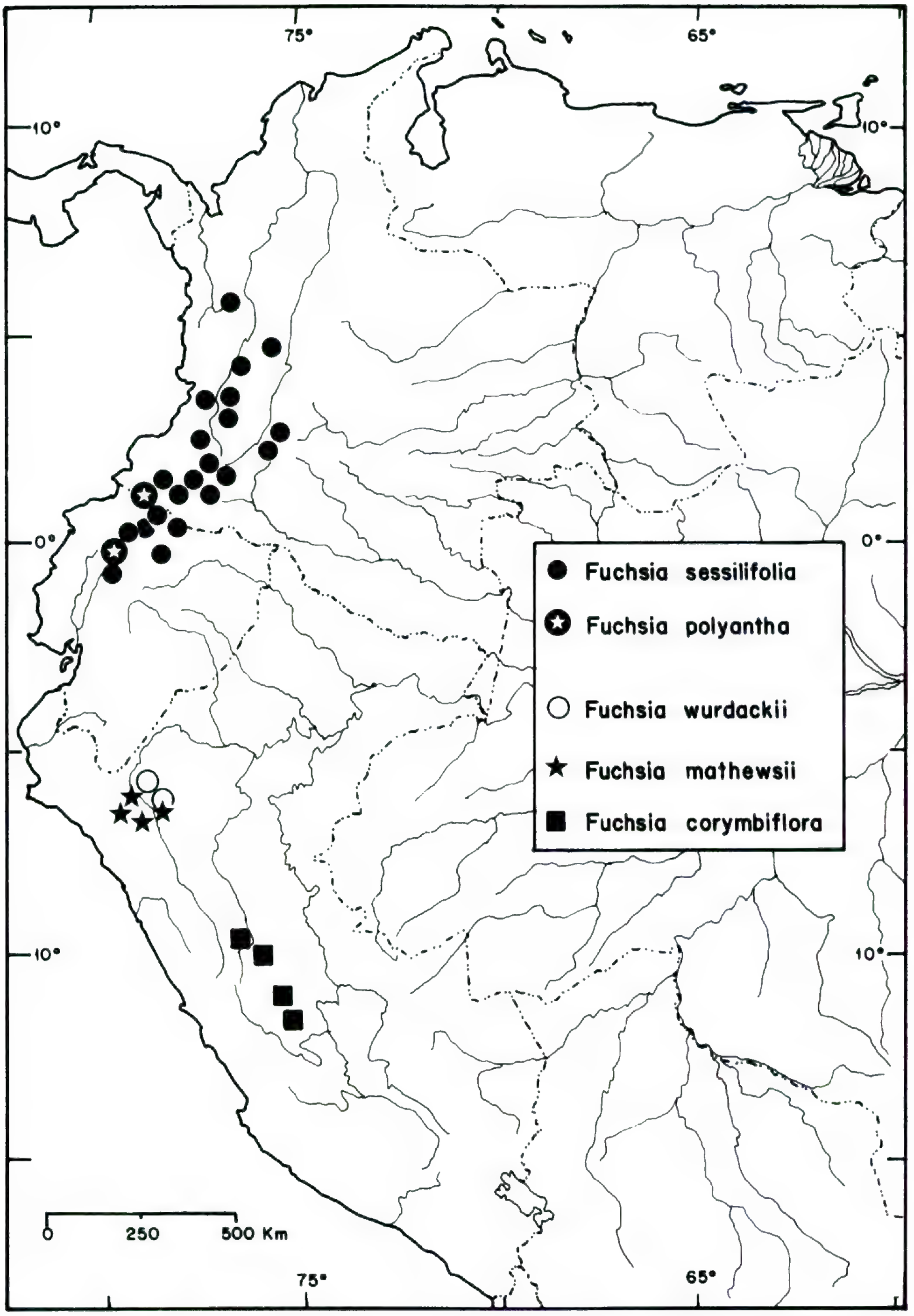


FIGURE 63. Distribution of the *Fuchsia sessilifolia* species group and part of the *F. boliviana* species group.

red, a little darker than the sepals, lanceolate to narrowly elliptic, subacuminate, 8–14 mm long, 2.5–4 mm wide. Nectary unlobed, ca. 1 mm high. Filaments red, 8–11 mm and 6–7 mm long; anthers oblong, 2–2.5 mm long, ca. 1.5 mm wide. Style red, sparsely pilose in lower ½; stigma capitate, slightly 4-parted at the apex, 2–3 mm long, ca. 2 mm wide, dull white, exserted 3–4 mm beyond the anthers. Mature berries not seen, young ones oblong, 8–10 mm long, 5–7 mm thick. Gametic chromosome number $n = 11$.

Distribution: Western slopes of the Cordillera Occidental from Nariño, Colombia south to Pichincha, Ecuador; rare in cloud forest, 2,200–3,300 m (Fig. 63).

Specimens examined: ECUADOR, CARCHI: 50 km W of Tufiño on road to Maldonado, *Berry 3152* (MO, QCA); 60 km W of Tufiño to Maldonado, *Berry 3154* (MO, QCA); 20 km E of Maldonado on road to Tulcán, *Gentry & Shupp 26321* (MO); between Morán and Olivos, *Mexia 7474* (US). PICHINCHA: Km 32–38 of old road from Quito to Santo Domingo de los Colorados, *Luteyn & Lebrón-Luteyn 5620* (MO, NY).

Except for its longer, entirely red flowers, this species is very similar to the more widespread and apparently sympatric *Fuchsia sessilifolia*. They both have distinctive subsessile, narrow, quaternate leaves with a well branched, terminal, drooping inflorescence. No plants with intermediate flower tube sizes or colors have been seen, and the two species may be reproductively isolated by different pollinators. The floral tubes of *F. sessilifolia* are greenish and less than 20 mm long, while those of *F. polyantha* are red and 34–43 mm long.

46. Fuchsia tincta I. M. Johnston, J. Arnold Arbor. 20:242. 1939. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):565. 1941, pro parte. Munz, Proc. Calif. Acad. Sci. IV. 25:43, *pl. 6, fig. 32*. 1943, pro parte. TYPE: Peru, Dept. Cuzco, Prov. Paucartambo, Río Tambomayo, 1,800–2,000 m, 25 July 1936, *James West 7092* (UC, holotype, not seen; photograph of GH isotype, NY; GH, MO, isotypes).

Erect subshrubs 0.5–1.5 m tall. Young growth whitish pilose, turning tan to reddish-brown with age; older stems 4–10 mm thick, with light brown, striated bark. Leaves opposite or sometimes subopposite near the branch tips, softly membranous, ovate-elliptic to broadly ovate, acute to rounded or unequal at the base, acute to acuminate at the apex, 3–14 cm long, 1.5–9 cm wide, velvety dark green and strigillose above, pale green or commonly purple flushed and strigose below, pubescence denser along the nerves; secondary veins 11–18 on either side of the midvein, sulcate above; margin glandular-denticulate to coarsely dentate. Petioles strigose, 13–50 mm long. Stipules lanceolate, dark, 1–2 mm long, subpersistent. Flowers usually 5–10 and nodding in a generally compact, terminal, corymbose raceme; rachis 1.5–7 cm long. Pedicels slender, strigose, 18–30 mm long, ascending in bud to divergent at anthesis. Ovary cylindric-fusiform, 6–8 mm long, 1–2 mm thick. Floral tube narrowly funnelform, 16–23 mm long, 1.5–2.5 mm wide and slightly bulbous at the base, narrowed to 1–1.5 mm above the nectary, then widened gradually above until 3–5 mm wide at the rim, pilose outside, retrorse villous inside in lower ½. Sepals lanceolate, 7–9 mm long, 3–4 mm wide, acute, spreading at anthesis. Tube and sepals pink to bright red. Petals pink to red, oblong, 6–9 mm long, 3–5 mm wide, obtuse to mucronate at the

TABLE 13. Principal morphological differences between *Fuchsia tincta* and *F. vargasiana*.

	F. tincta	*F. vargasiana*
Leaves:		
Shape	Broadly elliptic-ovate	Narrowly elliptic-ovate to deltoid
Color	Dark green above, mostly purple flushed below	Medium-dark green above, pale green below
Flowers:		
Tube length	12–23 mm	35–40 mm
Sepal color	Red pink	Dull green
Sepal and petal angle at anthesis	Spreading	Strongly spreading to divergent
Fruits:		
Shape	Ellipsoid to subglobose	Narrowly cylindrical, often curved and with a constricted apex
Length when ripe	13–17 mm	25–32 mm

apex, spreading at anthesis. Nectary unlobed or shallowly 4-lobed, ca. 1.5 mm high. Filaments pink to red, 5–7 mm and 3–4 mm long; anthers oblong, ca. 2 mm long, ca. 1.2 mm wide, white. Style light red, retrorse villous in lower ⅔; stigma capitate, 1.5–2 mm long, 1.5–2 mm wide, 4-parted at the apex, white to light pink, exserted 2–3 mm beyond the anthers. Berry ellipsoid to subglobose, 13–17 mm long, 8–11 mm thick; seeds 1.4–1.6 mm long, ca. 1 mm wide. Gametic chromosome number $n = 11$.

Distribution: Endemic to Dept. Cuzco, Peru. Locally common in damp, shady thickets along streams and roadsides, on the eastern slopes of the Andes in the Pillahuata area, between Paucartambo and Pilcopata; also known from Prov. Convención farther north; 1,800–2,400(–2,800) m (Fig. 62).

Specimens examined: PERU, CUZCO: Km 131–137 of Cuzco-Pilcopata road, near Buenos Aires, *Berry et al. 2597* (MO, USM), *3004* (MO, USM), *3006* (MO, USM); Pillahuata, Cerro de Cusilluyoc, *Pennell 13956* (F, GH, PH, S, US); above Pintobamba, Prov. Convención, *Vargas 3551a* (BH, CUZ); Pillahuata, *Vargas 5128* (BH, CUZ, MO); Ticancha, Huaisanpilla, *Vargas 9922* (CUZ, MO); Pillahuata, Yanamayo, Va*gas 16695* (CUZ, RSA), *16703* (CUZ, RSA), *Woytkowski 2* (MO, USM); between Puente Mercurio and Buenos Aires, *Vargas 23138* (MO); Suecia, *Woytkowski 144* (USM).

This species is closely allied to *Fuchsia vargasiana* and *F. furfuracea,* which share the compact, terminal racemes, dense pubescence, and similar ovate, long-petiolate leaves. *Fuchsia tincta* has shorter flowers than these two species, though, and usually has deep dark green leaves with a purple flush below.

It is remarkable that *F. tincta* and *F. varagasiana* are so similar morphologically, yet they are sympatric and occupy the same restricted range. Both are diploid and grow together in the same thickets at ca. 2,100 m (Km 136–137) along the Paucartambo-Pilcopata road, flowering simultaneously. Despite this, no apparent hybrids or morphological intermediates were found either in the field or

TABLE 14. Comparison of the principal morphological differences between *Fuchsia tincta*, *F. sanctae-rosae*, and a presumed hybrid.

	F. tincta	Hybrid (*Pennell 13956*, NY)	*F. sanctae-rosae*
Leaves:			
number/node	2	2–3	3–4
Max. blade size (L × W)	14 × 9 cm	15 × 6 cm	14 × 4 cm
Pubescence, lower surface	Strigose on entire surface	Strigose mostly along veins	Glabrous except hairs on midvein
Flowers:			
Position	Racemose	Axillary	Axillary
Tube pubescence outside	Pilose	Strigose-pilose	Glabrous
Pubescence on young growth	Whitish pilose	Canescent	Subglabrous

in herbarium specimens. An enumeration of the main differences between *F. tincta* and *F. vargasiana* is presented in Table 13.

Fuchsia tincta is also sympatric with *F. sanctae-rosae*. *Pennell 13956* (NY), from Pillahuata, is apparently a hybrid between these two species. Diagnostic characters of the putative hybrid and the parental species are given in Table 14. A pollen stainability of 9.2% (500 grains examined) for this collection further supports the hypothesis that it is of hybrid origin.

47. Fuchsia furfuracea I. M. Johnston, Contr. Gray Herb. 75:39. 1925. Munz, Proc. Calif. Acad. Sci. IV. 25:46, *pl. 6, fig. 34*. 1943. TYPE: Bolivia, Dept. La Paz, Yungas, 1890, *Miguel Bang 674* (BH, holotype; photographs, POM, UC; F, K, MO, NY, PH, US, isotypes).

Erect to scandent shrubs 0.5–2.5 m tall. Young growth densely hispidulous to tomentose with suberect, whitish hairs often becoming tan or ferrugineous with age or drying; branchlets subterete, 2–4 mm thick, green or reddish; older branches 5–10 mm thick, loosly hirtellous, with smooth, purple tan bark. Leaves opposite or rarely ternate, membranous, elliptic-ovate, rounded to acute at the base, acuminate and often curved at the apex, 6–15(–17) cm long, 3–6(–7) cm wide, matte dark green and hispidulous-strigose above, slightly paler to flushed purple and hispidulous below, especially along the nerves; secondary veins 9–14 on either side of the midvein, subelevated below; margin serrulate to denticulate. Petioles pubescent, 2–5(–7) cm long. Stipules lance-linear, acuminate, dark, 2–3 mm long, 0.2–0.4 mm wide. Flowers few and pendant in short, corymbiform, terminal racemes; rachis 1.5–5 cm long with bracts 10–25 mm long. Pedicels slender, pubescent, 15–40 mm long, lengthening considerably from bud to fruit. Ovary ellipsoid-oblong, 5–8 mm long, 2–3 mm wide, densely pubescent. Floral tube narrowly funnelform, (22–)25–48 mm long, 2–3 mm wide and slightly nodose at the base, constricted to 1.5–2 mm wide above the nectary, gradually widened above until 6–9 mm wide at the rim, hispidulous outside, villous inside for most its length. Sepals lanceolate, 10–18 mm long, 3–5 mm wide, mostly long acuminate with free tips in bud for 1–3 mm, spreading at anthesis. Tube dull pink to lavender

TABLE 15. Comparison of morphological characters in *Fuchsia furfuracea*, *F. sanctae-rosae*, and presumed hybrids.

	F. furfuracea (*6744*, BM, F)[1]	Hybrids (*6653*, BM, F) and (*6693*, BM)[1]	Hybrids (*6719*, BM, F)[1]	*F. sanctae-rosae* (*6653*, NY) and (*6693*, F, NY)[1]
Stem pubescence	Densely pilose, reddish hairs	Loose villous	Loose villous	Glabrous
Leaf shape	Broadly ovate	Lance-elliptic	Narrowly elliptic	Narrowly elliptic
Leaf pubescence	Strigillose on both sides	Densely villous on veins below	Villous on both sides	Glabrous except hairs on mid-vein below
Leaf margin	Serrulate	Lightly serrulate	Serrulate	Entire
Number of secondary veins	11–18	10–16	11–12	5–10
Inflorescence type	Tight terminal raceme 1–4 cm long	Subracemose, 6–12 cm long	Subracemose, 8–16 cm long	Axillary along uppermost 25 cm of branches

[1] All numbers refer to W. Brooke collections from Incachaca, Dept. Cochabamba, Bolivia, collected in Aug. 1950.

or orange red; sepals light red but becoming pale white toward the tips. Petals bright pink red to dark red, elliptic-ovate, mostly about ½ as long as the sepals, 6–10 mm long, 3–5 mm wide, acute at the apex, suberect at anthesis. Nectary unlobed or shallowly 4-lobed, ca. 1.5 mm high. Filaments lavender, 7–8 mm and 4–5 mm long; anthers oblong, 2–3 mm long, 1–1.5 mm wide. Style villous from the base to near the rim of the tube; stigma capitate, 4-cleft at the apex, 2–3 mm long, 2–3 mm wide, white. Berry ovoid-ellipsoid, becoming subglobose when fully ripe, 12–16 mm long, 6–12 mm thick, pubescent; seeds ca. 1.5 mm long, ca. 1 mm wide.

Distribution: Bolivia. Rare shrubs growing mostly in dripping wet sites such as cliff overhangs and along rivulets in cloud forest of Depts. La Paz and Cochabamba; 2,800–3,050 m (Fig. 62).

Specimens examined: BOLIVIA, COCHABAMBA: Incachaca, *Brooke 6744* (BM, F). LA PAZ: San Felipe, Sur Yungas, *Asplund 1743* (UPS); near Chuspipata, Km 65 of La Paz-Beni RR, *Barker 220* (US); valley of Zongo, Prov. Murillo, *Beck 2173* (MO); 9 km from Unduavi on road to Coroico, *Berry 2577* (MO); Unduavi, *Cárdenas 3617* (RSA); Carretera Fundamental 3, 27 km SW of Yolosa junction, *Davidson 4937* (MO); Unduavi, *Rusby 2511* (NY); 20 km SW of Yolosa junction toward Unduavi, *Solomon 4860* (MO), *4865* (MO); Yungas valley, *Tutin 1391* (BM); 19 km from Unduavi to Coroico, *Vargas 22057* (CUZ); Prov. of Yungas, *Weddell 2291* (P); valleys between Tipuani and Apolobamba, Prov. Larecaja and Caupolicán, *Weddell 4601* (P). WITHOUT LOCALITY: *Bridges 283* (LE), *in 1846* (BM, CGE, K); *Cuming 229* (W), *s.n.* (W).

The few-flowered, compact, terminal inflorescences and mostly opposite, pubescent, long petiolate, ovate leaves closely ally this species to *Fuchsia tincta* and *F. vargasiana*, both of which are endemic to southern Peru. The flowers of *F. furfuracea* are larger than those of *F. tincta*, and the fruits are shorter than those of *F. vargasiana*. *Fuchsia furfuracea* is further characterized by its elongate stipules, mostly ferrugineous hairs on older growth, and pale sepals usually about twice as long as the petals.

All three species in the *F. tincta* species group have a very restricted range.

TABLE 16. Pollen stainability of *Fuchsia furfuracea*, *F. sanctae-rosae*, and suspected hybrids.[1]

Taxon	Stainability[2]
Fuchsia furfuracea (*Brooke 6744*, BM, F)	88.4%
Hybrid (*Brooke 6693*, BM)	0%
Hybrid (*Brooke 6719*, BM)	20%
Hybrid (*Brooke 6653*, F)	8.6%
Fuchsia sanctae-rosae (*Brooke 6653*, NY)	83.8%

[1] All specimens collected in Aug. 1950, around Incachaca, Dept. Cochabamba, Bolivia.
[2] 500 grains counted for each collection.

Fuchsia furfuracea is known from a few localities in the "yungas," or moist, cool valleys of the northeastern slopes of the Bolivian Andes, and it is furthermore restricted to very moist habitats such as streamsides or near waterfalls.

Weddell 4061 (P), from Prov. Larecaja near the Peruvian border, has floral tubes just 22 mm long and is distinguishable from *F. tincta* only by its slightly longer, browner pubescence and proportionately shorter petals. There are no other collections from the Peru-Bolivia border area, however, to indicate if more intergradation between these two species occurs there.

In Dept. La Paz, *Fuchsia furfuracea* is found close to, but at higher elevations than *F. boliviana* and *F. sanctae-rosae*; it occurs at lower elevations than *F. denticulata*. In Dept. Cochabamba, a series of probable hybrids with *F. sanctae-rosae* were collected by Winifred Brooke in 1950 around Incachaca. Intermediate morphological traits of the putative hybrids are compared to those of the presumed parents in Table 15, and Table 16 shows the strongly reduced pollen stainability of the same intermediates. I returned to Incachaca in July 1979 and found plants of *F. sanctae-rosae* abundant in weedy thickets, but no trace of *F. furfuracea*. The valley at Incachaca is now mostly cleared or covered by secondary vegetation, and *F. furfuracea* is confined to more heavily forested areas.

48. Fuchsia vargasiana Munz ex Vargas, Diez Años Servic. Bot. Univ. Cuzco, 50, *fig. 16*. 1946. TYPE: Peru, Dept. Cuzco, Prov. Paucartambo, between Yanamayo and Tambomayo, 2,000 m, 25 July 1936, *César Vargas C. 73* (BH, holotype; CUZ, F, MO, POM, isotypes). On the type sheet, Vargas indicated that the same plant was collected by James West, under a separate number, *West 7110* at GH and UC.

Fuchsia tincta sensu J. F. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):564. 1941, pro parte, sensu Munz, Proc. Calif. Acad. Sci. IV. 25:43. 1943, pro parte.

Erect shrubs 1–2 m tall. Young growth finely soft pilose with white to rusty hairs; older branches 4–10 mm thick, dull tan-brown. Leaves opposite, membranous, narrowly ovate-elliptic to narrowly subdeltoid, rounded to obtuse or unequal at the base, acuminate at the apex, 6–23 cm long, 2.5–9 cm wide, subnitid dark green and sparsely strigose to subglabrous above, pale green below and finely pilose mostly along the veins; secondary veins 12–18 on either side of the midvein; margin glandular-serrulate or denticulate. Petioles pubescent, 12–60 mm long. Stipules lanceolate, dark, 1–2 mm long, ca. 0.4 mm wide, deciduous. Flow-

ers usually 3–10 in terminal, corymbose racemes; rachis 2–8 cm long, at times with reduced leaves subtending the flowers. Pedicels ascending when young to divergent-drooping at anthesis, 10–35 mm long. Ovary narrowly cylindrical, puberulent, 10–11 mm long and ca. 2 mm thick. Floral tube narrowly funnelform, 35–40 mm long, 2–3.5 mm wide and slightly nodose at the base, narrowed to 1.5–2.5 mm above the nectary, then gradually widened above until 4–8 mm wide at the rim, pilulose outside, villous inside in lower ⅔. Sepals lanceolate, acuminate, 11–16 mm long, 4–5 mm wide, with a short tip 1–2 mm long in bud, strongly spreading to divergent at anthesis. Tube red, sepals green except for the reddish base. Petals red, oblong to broadly elliptic, 10–12 mm long, 5–8 mm wide, rounded and usually with a short point at the apex, strongly spreading at anthesis. Nectary unlobed, ca. 2 mm high. Filaments red, 6–10 mm and 4–8 mm long; anthers oblong, 2–3 mm long, 1–1.5 mm wide, white. Style red pink, villous from the base to near the rim of the tube; stigma capitate, ca. 2 mm long and wide, 4-parted at the apex, white to dull pink. Berry narrowly cylindrical-fusiform, often curved and usually constricted at the apex, 25–32 mm long, ca. 8 mm thick; seeds 1.3–1.6 mm long, 0.9–1.1 mm wide. Gametic chromosome number $n = 11$.

Distribution: Endemic to Dept. Cuzco, Peru. Locally frequent in moist shady thickets along the Río Tambomayo, Pillahuata area of Prov. Paucartambo; 1,700–2,300 m (Fig. 62).

Specimens examined: PERU, UZCO: Km 132–140 of Cuzco-Pilcopata road, below Buenos Aires, *Berry et al. 3000* (MO, USM), *3003* (MO), *3005* (MO, USM); between Yanamayo and Santa Isabel, valley of Río Cosñipata, *Scolnik 851* (RSA); Tambomayo, *Vargas 22986* (MO); Pillahuata, *Vargas 22985* (MO); Suecia, *Woytkowski 128* (USM).

This species is closely related to the sympatric *Fuchsia tincta* and to the Bolivian *F. furfuracea*. It has distinctive long, fusiform, curved fruits and narrower leaves than either of the above species, and its sepals are green-tipped. Its sympatric occurrence and apparent lack of intermediates with *F. tincta* are discussed under that species, and a comparison of their distinguishing characters is presented in Table 13.

The label of *Vargas 4524* (BH) records the collection locality as "Dept. Cuzco, Prov. Convención, 3,600 m," but this is probably in error, since it is very unlikely that this species would occur at so high an elevation. *Fuchsia vargasiana* is sympatric with *F. sanctae-rosae*, *F. tincta*, and populations of *Fuchsia* related to *F. denticulata* (Fig. 11).

49. Fuchsia boliviana Carrière, Rev. Hort. 48:150, *pl.* 1876. Hemsl., Garden 11:70, *pl.* 1877. Johnst., Contr. Gray Herb. 75:37. 1925. Fawc. & Rendle, Fl. Jamaica 5:413, *fig. 149*. 1926. Travis, Fuchsia Annual 1975:55, *photo*. 1975. non Britton, 1890. *Fuchsia boliviana* var. *typica* Munz, Proc. Calif. Acad. Sci. IV. 25:53, *pl. 8, fig. 42*. 1943. Based on *F. boliviana* Carr. TYPE: Plate in Révue Horticole 48:150. 1876, drawn from plants cultivated in France in 1876 from seeds collected in the mountains of Bolivia at "6000 m" (a probable error for 6,000 ft.) in 1873 by Benedict Roezl. Figs. 34, 43, and 64 (lectotype, here designated).

Fuchsia corymbiflora auct., non Ruiz & Pavón, 1802. Lindl., Bot. Reg. 26: *pl. 70*. 1840. Harrison,

Floric. Cab. & Florist's Mag. 9: *t. 1.* 1841. Paxt., Paxton's Mag. Bot. 8:7, *pl.* 1841. Hook., Bot. Mag. 69: *pl. 4000.* 1843; Gard. Chron. 1845:192, *fig.* 1845, Sweet, Ornam. Fl. Gard. 1: *t. 29.* 1854. Regel, Gartenfl. 28:241, *fig.* 1879. Sieb. & Voss. in Vilm., Bulmengart. ed. 3, 1:333, *fig.* 1896. Watson, Garden 55:74, *fig.* 1899. Hegi, Ill. Fl. Mittel-Eur. 5(2):801, *fig. 2189, a–d.* 1925. Bonstedt in Pareys Blumengart. 2:79, *photo.* 1932. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):551. 1941, pro parte.

Fuchsia corymbiflora alba Harrison, Floric. Cab. Florist's Mag. 17:97, *fig.* May, 1849. Paxt., Paxton's Mag. Bot. 16:219. 1849. van Houtte, Fl. Serres Jard. Eur. 6:29, *fig.* 1850. Essig. Nat. Hort. Mag. 13:6, *photo.* 1934. LECTOTYPE: the figure in Harrison, Floric. Cab. Florist's Mag. 17:97. 1849, illustrated from plants grown by John Salter in 1849 in London, England from plants obtained from "Continental Europe."

Fuchsia boliviana var. *luxurians* I. M. Johnston, Contr. Gray Herb. 75:37. 1925. Munz, Proc. Calif. Acad. Sci. IV. 25:54. 1943. TYPE: Venezuela, Edo. Aragua, Colonia Tovar and vicinity, 1,700–2,300 m, 19 Feb. 1921, *Henry Pittier 9252* (GH, holotype; photograph, UC; NY, US, VEN, isotypes).

Fuchsia cuspidata Fawcett & Rendle, Journ. Bot. 114:105. 1926. TYPE: Jamaica, Blue Mountains, near Woodcutter's Gap, ca. 1,200 m, 10 Aug. 1895, *William Harris 5825* (BM, holotype).

Fuchsia boliviana forma *puberulenta* Munz, Proc. Calif. Acad. Sci. IV. 25:54. 1943. TYPE: Bolivia, Dept. La Paz, Prov. Nor Yungas, 1,800 m, Dec. 1917, *Otto Buchtein 732* (F 588700, holotype; photographs, POM, UC; F, G, GH, MO, NY, US, Z, isotypes).

Erect bushy shrubs or small trees 2–4.5(–6) m tall with arching-pendulous branches. Young growth usually densely canescent with fine, erect, gray-white hairs; terminal shoots 2–4 mm thick, terete to angled; older stems woody, usually hollow, 1–6 cm thick, with tan brown, splitting bark. Leaves opposite, ternate, or sometimes alternate near the uppermost branching nodes, softly membranous, narrowly to broadly elliptic or ovate, acute to rounded at the base, acute to acuminate at the apex, 5–20(–23) cm long, 3–12(–15) cm wide, medium to dark matte green and pubescent to subglabrous above, pale green and ashy puberulent to densely canescent below, especially along the nerves; secondary veins (12–)15–25 on either side of the midvein, ± impressed above, prominent and often reddish below; margin glandular-denticulate. Petioles pubescent, 2–5(–7) cm long. Stipules dark, narrowly lanceolate, 0.5–1.5 mm long, ca. 0.3 mm wide, deciduous. Flowers numerous in terminal, drooping racemes or few-branched panicles, the flowers congested near the tips; rachis 5–30 cm long in flower, 15–40(–60) cm long in fruit; bracts lanceolate, reflexed, 5–25 mm long, 2–8 mm wide. Pedicels slender, pendant, pubescent, 5–12(–16) mm long. Ovary cylindrical, 7–11 mm long, 2–3 mm thick, strigose to puberulent. Floral tube narrowly funnelform (25–)30–60(–70) mm long, 1.5–3 mm wide and slightly bulbous at the base, gradually widened above until 4–7(10) mm wide at the rim, pubescent outside, pilose inside for entire length. Sepals lanceolate, acuminate, 10–20 mm long, 4–5 mm wide, tips apiculate in bud, initially spreading at anthesis, but soon becoming totally reflexed. Tube and sepals pale pink to bright scarlet, rarely pale white. Petals scarlet, acute at the apex, ± crispate with 2–3 longitudinal ridges, oblong to elliptic, 8–16(–20) mm long, 3–7(–9) mm wide, upper ½ recurved at anthesis, drying and dehiscing before the tube does. Nectary 4-lobed, green, 2–3 mm high. Filaments red, 8–15 mm and 5–10 mm long; anthers oblong, 2–3.5 mm long, 1–1.5 mm wide, white. Style slender, pilose from the base to the rim of the tube; stigma capitate or clavate, subtetragonous, shallowly 4-lobed at the apex, 2.5–3 mm long, 3–5 mm wide, cream, situated at the level of the antesepalous anthers or barely exserted beyond them. Berry cylindrical, 10–26 mm long, 8–14 mm thick, dark purple, strigose, comestible; seeds tan, 1.3–2 mm long, 0.5–1 mm wide. Gametic chromosome number $n = 11$.

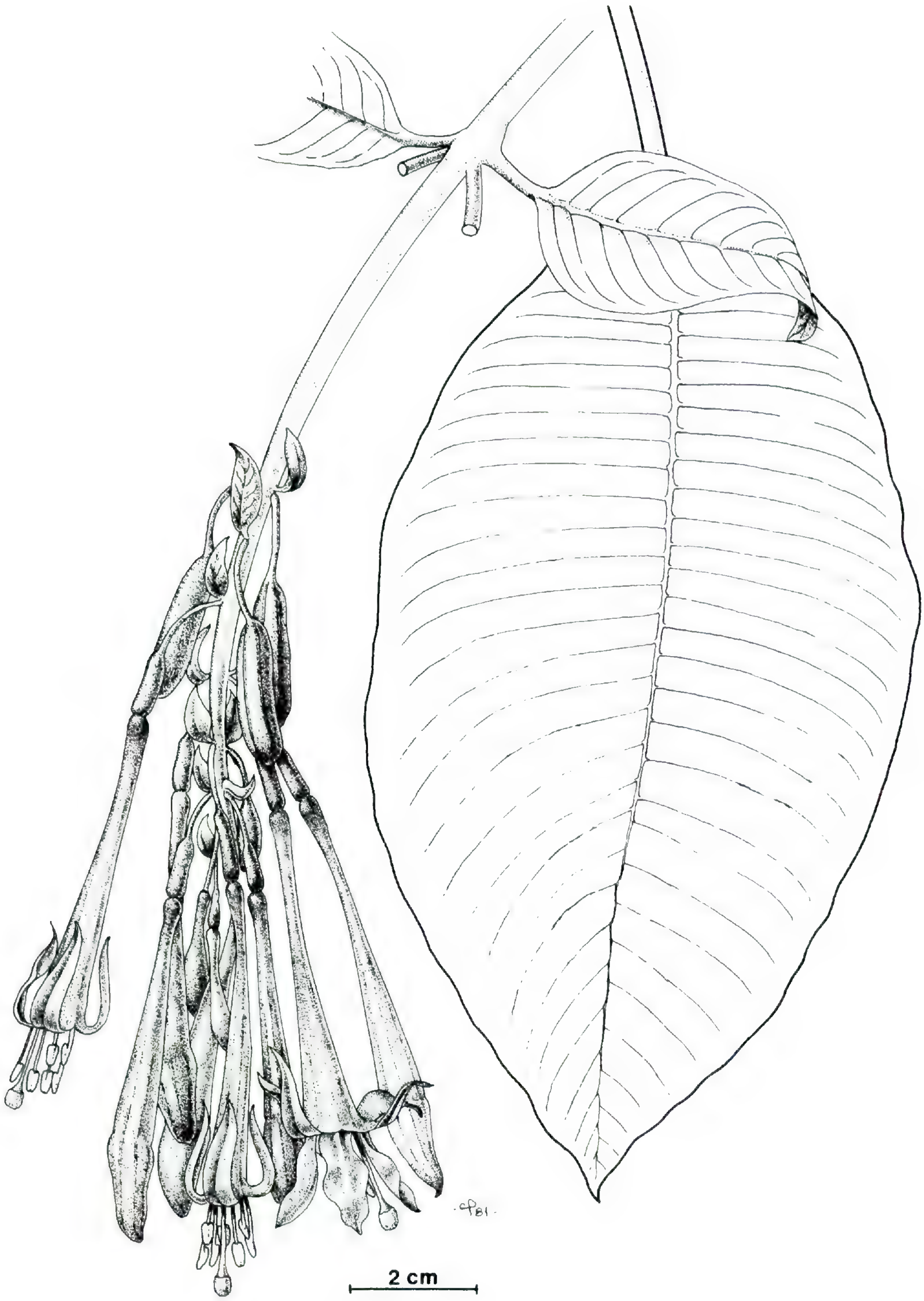


FIGURE 64. *Fuchsia boliviana* Carrière. Drawn from living material from El Portachuelo, D.F., Venezuela.

Distribution: The probable native range extends from northern Argentina to southern Peru, undoubtedly naturalized elsewhere outside South America and in Colombia and Venezuela; cloud forest shrubs in moist thickets; (600–)1,000–3,000 m (Fig. 65).

Representative specimens examined (South America): VENEZUELA, ARAGUA: Colonia Tovar, *Agostini 65* (VEN), *Allart 354* (MY, NY, US, VEN), *Berry 2592* (MO, VEN), *Fendler in 1854–55* (K), *Jahn 439* (US), *Woronow 7048* (LE); between El Lagunazo and Colonia Tovar, *Aristeguieta 781* (VEN), *Trujillo & Fernández 852* (MY); La Victoria to Colonia Tovar, between Las Moras and Lagunita, *Benítez de Rojas 566* (MY); Hacienda El Limón, Las Aguaitas, *Delascio 2057* (VEN); between Colonia Tovar and Pico Codazzi, *Ruiz-Terán & López-Palacios 10118* (MERF, MO); La Lagunita, near Colonia Tovar, *Schnee 1309* (MY), ca. 5 km from Colonia Tovar towards El Limón, *Solymosy S10197150* (VEN). DISTRITO FEDERAL: between El Junquito and Colonia Tovar, *Berry 2591* (MO, VEN), *Wessels-Boer et al. 2445* (MO, U); 1–2 km below junction of El Junquito-Colonia Tovar road towards Carayaca, *Cárdenas de Guevara 433* (MY), *Davidse & Morillo 3985* (MO), *Luteyn et al. 5162* (MO, NY); 4 km ENE of Colonia Tovar, *Steyermark 86212* (MY, NY, VEN). COLOMBIA, ANTIOQUIA: Las Minas, *Barkley 17C250* (GH); near Boquerón del Toyo, *Barkley & Neira 17C235* (CAS, COL, GH); canyon 20 km E of Sonsón, road to El Dorado, *Barkley 38C568* (COL, GH); Alto de Minas, Medellín to La Pintada, *Escobar 1000* (MO); near San José de San Andrés, *Correa & Velásquez 68* (COL, RSA, US); between Alto San Miguel and Alto Alegrías, 15 km SSE of Caldas, *Fosberg 21163* (NY, RSA, US); Alto de Minas, between Caldas and Santa Bárbara, *Garganta 2003* (US); El Poblado, near Medellín, *Hatheway in 1955* (B); Las Minitas, S of Caldas, *Pennell 10970* (GH, NY); Cerro del Pedre Amaya, Boquerón, Km 22 of Medellín-Santa Fé de Antioquia road, *Rivera 808* (PSO). CALDAS: Termales, *Dryander 2756* (BH, F, VALLE); Manizales, *Sandeman 5655* (COL, K). CHOCÓ: N of Albán, near Dept. Valle border, *Dugand & Jaramillo 3046* (US); 2–3 km N of Carmen de Atrato, *Fosberg & Core 21553* (RSA, US). CUNDINAMARCA: 2.5 km W of Salto de Tequendama, *Barclay et al. 3303* (COL, NA, US), *Luteyn & Lebrón-Luteyn 7711* (COL, MO, NY); Bogotá, *Duque-Jaramillo 3049* (COL, NY), *Pérez-Arbelaez 4802* (NY, U, US); 17 km W of Mosquera towards La Mesa, *Gentry 15139* (COL, MO); Km 26–28 SW of La Mosquera towards La Mesa, *Luteyn et al. 4690* (COL, MO); Zipaquirá, *Pring 168* (MO); Bogotá, Chapinero, *Schneider 353-A* (COL); 2 km from Zipaquirá on road to Pacho, *Schultes et al. 3* (GH, K, S, US). SANTANDER: 24 km W of Jordán on Cimitarra-Velez road, *Gentry & Forero 15466* (COL, MO); 29 km W of Fresno towards Manizales, *Berry 3552* (COL, MO); above Cajamarca, Giradot-Armenia road, *Berry 3143* (MO); La Palmilla, Quindío, *Triana 3812* (G, P); Herveo, *Uribe-Uribe 756* (COL). VALLE: N of Las Brisas, Carrizales, *Cuatrecasas 22552* (F, RSA, VALLE). PERU, APURIMAC: Abancay, *Blood & Tremelling 206* (NA): Chincheros, *Ferreyra 2810* (USM), *Soukup 6248* (RSA); 8 km E of Abancay, road to Cuzco, *Gentry et al. 23368* (MO); Ampuy, *Stork et al. 10595* (A, G, MO, NA, UC); Chirhuay-Matará, *Vargas 1971* (BH, CUZ, MO); Nacchero, *Vargas 8962* (CUZ); Huancarema, *West 3783* (MO, UC). AYACUCHO: 11 km below Jano, road Tambo-Ayna, *Berry 3057* (MO, USM); Ccarrapa, between Huanta and Río Apurimac, *Killip & Smith 22280* (NY, RSA, US); above Jano, *Plowman & Davis 4673* (GH, K); Curahuasi, *Sandeman 3552* (K, OXF); Ocros, *Vargas 15912* (CUZ); Prov. La Mar, *Weberbauer 5555* (F, GH, US). CUZCO: Paucartambo, *Balls B6715* (BM, K, NA, UC, US), *Plowman & Davis 4910* (GH); Urubamba, *Berry 2561* (CUZ, MO), *Herrera 1058* (GH, US), *Soukup 28* (F), Km 169 of Cuzco-Quillabamba road, *Berry & Aronson 3044* (MO, USM); San Miguel, *Chávez 3108* (MO), *Cook & Gilbert 915* (US); Hacienda Santa Rita, Urubamba valley, *Dreyfus in 1941* (USM); Machupichu, *Ferreyra 2728* (USM), *Rauh 773* (RSA), *Vargas 990* (BH, CAS, CUZ, MO); Lucay, Urubamba valley, *Herrera 1123* (F, US); Hacienda Churu, Prov. Paucartambo, *Herrera in 1926* (US); Km 105 along RR in Urubamba valley between Ollantaytambo and Machupichu, *Iltis & Ugent 1132* (DS, GH, K, UC, USM); Punto Real, Urubamba valley, *Tutin 1308* (BM); Ollantaytambo, *Tutin 1340* (BM); 5 km NE of Paucartambo on road to Pillahuata, *Ugent & Vargas 4410* (DS); Huaisanpilla, *Vargas 9945* (CUZ); Mantla, Km 84, Prov. Calca, *Vargas 15630* (CUZ); Urubamba valley, between La Máquina and Cedrobamba, *West 3783* (GH, MICH, MO, NA, RSA, UC, US, USM); Pilco, valley of Río Paucartambo, *Woytkowski 320* (MO, UC); near Chacra, Prov. Paucartambo, *Woytkowski 236* (USM). HUÁNUCO: 5 km SE of Carpish, *Stork & Horton 9921* (F, MICH, MO, RSA, UC, US). PUNO: near Sandia, *Ferreyra 16652* (MO); Oconeque, E of Limbani, *Hodge 6166* (US); Asalaya, *Vargas 11812* (CUZ); near Sandia, *Vargas 14808* (CUZ), *16414* (CUZ), *21246* (CUZ), *Weberbauer 537* (G), *557* (G). BOLIVIA, COCHABAMBA: Km 205 Cochabamba-Santa Cruz, *Badcock 382* (K); ca. 60 km from Cochabamba to Villa Tunari, *Berry 2588-B* (MO); Quime, ca. 160 km from Oruro via Eucalyptus, Quimicruz mts., *Brooke 5385* (BM, F), *5418* (BM); Rosal, near Río Limón, *Brooke 5706* (BM, F, G, NY, U), *5719* (BM, F); Choro, above Río Cocapata, ca. 160 km NW of Cochabamba, *Brooke 6076* (BM, F, G, NY, S, U); Incachaca,

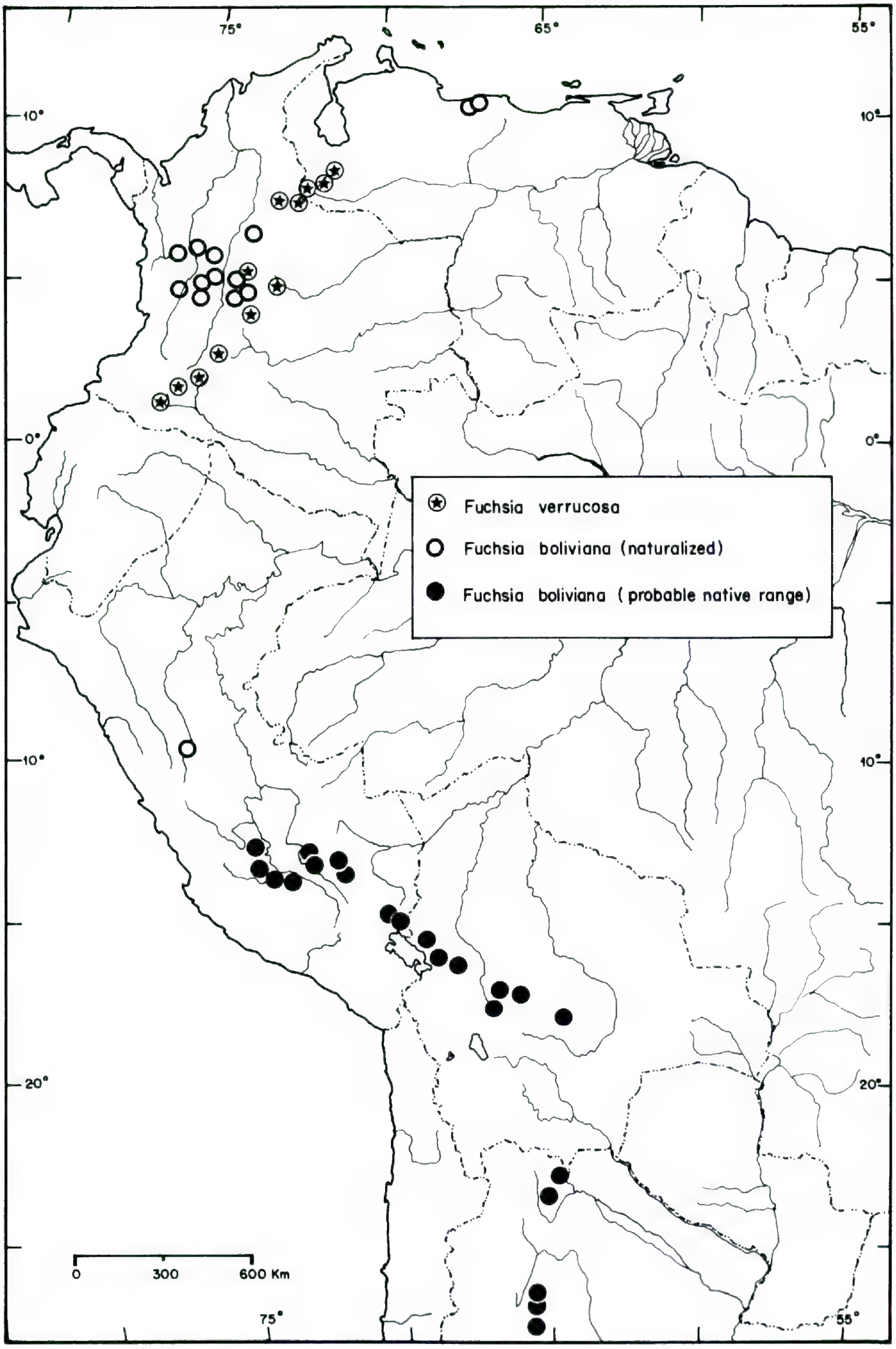


FIGURE 65. Distribution of *Fuchsia boliviana* and *F. verrucosa*.

Brooke 6653 (BM), *6670* (BM, F, NY), *6680* (BM, F), *6719* (BM), *Steinbach 4306* (K), *5024* (A, G), *5763* (A, F, G, GH, K, MO, PH, US); Parangani, Ayopaya, *Cárdenas 4086* (GH, RSA); 110 km NE of Cochabamba, near Chimore, S side Río Mateo, *Eyerdam 24740* (F, UC); Pocona-Tal, *Steinbach 8781* (BM, GH, K, MO, NY, S); El Limbo, *Steinbach 537* (G, GH, MO, NY, U, US). LA PAZ: Chungamayo, La Sirena, *Asplund 317* (UPS); El Chaco, Sur Yungas, *Asplund 1131* (UPS); Yungas, *Bang 327* (BM, F, GH, K, LE, MICH, MO, NY, PH, US, W); Zongo Valley, Prov. Murillo, *Beck 2172* (MO), *2739* (MO); Huancané, Sud Yungas, *Beck 3066* (MO); 13 km from Unduavi to Coroico, *Berry 2579* (MO); Chulumani, *Brooke 6560* (BM); Sirupaya, near Yanacachi, Sur Yungas, *Buchtein 102* (NY), *218* (NY, US); Sorata, *Cárdenas 1156* (NY); 15 km SW of Yolosa junction, *Davidson 4913* (MO); Caranavi, *Ellenberg 6217* (GOET); near Unduavi, *Eyerdam 25395* (F, UC); El Chaco, Sur Yungas, *Holway & Holway 643* (US); between Puente Villa and Chulumani, *Kelley 1013* (CM, UC); Sacramento, Unduavi to Coroico, *Kelley 1075* (CM, F, UC); near Sorotá, *Mandon 622* (BM, F, G, GH, K, LE, NY, P, S, T, US, W); Nor Yungas, *Mexia 04286* (GH, MO, UC); Colaya, Sur Yungas, *Mexia 04292* (G, GH, MO, UC), *7809* (F, G, K, MO, S, U, UC, US); near Yungas, *Rusby 1071* (BM, F, GH, K, LE, MICH, NY, P, PH, US); Okara, *Tate 908* (NY); Prov. Apopaya, *Weddell 4179* (P). SANTA CRUZ: Samaipata, *Steinbach 3755* (GH, POM); Yungas de San Mateo, *Steinbach 8392* (BM, GH, K, NY, S); Comarapa, *Steinbach 8459* (BM, GH, K, MO, NY, S). WITHOUT LOCALITY: *Bang 1806* (BM, F, G, GH, K, LE, MICH, MO, NY, PH, US, W, Z); *Bang 2005* (BM, F, GH, K, MO, NY, US, W); *Bang 2833* (F, GH, K, LE, MICH, MO, NY, PH, US). ARGENTINA, JUJUY: road to Valle Grande, Dep. Ledesma, *Cabrera et al. 22390* (K); San Lorenzo, *Jörgensen in 1911* (POM); 10–20 km from Libertador Gral. San Martín, road to Valle Grande, *Krapovickas et al. 26668* (MO); Valle Grande, ca. 2 km past Abra de Cañas, *Legname & Cuezzo 8601* (GH); Abra de Cañas, road to Valle Grande, *Vervoorst & Cuezzo 7851* (W). SALTA: San Andrés, *Lorentz & Hieronymus 265* (G, S), *Pierotti 312* (A, NY, UC). TUCUMÁN: Quebrada de Las Sosas, *Bocher et al. 2419* (MO, S), *Killip 39530* (RSA, US), *Walter & Walter 621* (B), *653* (B); Casa de Piedras, ca 25 km SSW of Tucumán, *Colaris 1181* (U); along Río Las Sosas, ca. 60 km SW of Tucumán, *Haas 893* (U); Sierra de Aconquija, *Humbert 20929* (P, US); Río Cicerone, *Jörgensen 21* (GH, MO); Km 20 road to Tafi del Valle, *Legname 96* (CAS, MO, W); Río Cochuna, Chicligasta, *Lillo 1510* (GH), *O'Donnell 10429* (BM, F, UC); Quebrada Caspinchango, *Lillo 7340* (GH), *Venturi 9598* (A, S); road to Tafí del Valle, Monteros, *Lourteig 450* (A, U, US); Villa Nougués, above Tucumán, *Munz 15469* (GH, NY, POM, US); from San Javier to Villa Nougués, *Ortiz in 1945* (A, BM, UC); Quebrada de Lules, *Quiroga 7215* (F), *Venturi 1295* (BM, CAS, F, GH, K, MO, RSA, UC, US, W), *2232* (A, POM, US, Z); Quebrada de Lules, Arroyo Grande, *Sleumer 759* (B); Estancia Las Pavas, Dept. Chichligasta, *Venturi 4657* (A, F, US). BRAZIL: Porto Alegre, cultivated, *Revicely in 1898* (W). CHILE: Jardín Suizo, Las Zorras, Valparaiso, cultivated, *Harshberger 1046* (P, US); Prov. Concepción, cultivated, *Junge 2975* (US).

Naturalized or cultivated specimens outside of South America: AZORES: Pico Island, above San Roque, *Brooke 11337* (BM); Graciosa, Praia, Santana, *Gonçalves 3113* (BM). COSTA RICA, ALAJUELA: Zarcuo, *A. Smith 2775* (F). CARTAGO: Cartago, *Donnell Smith 4804* (US). SAN JOSÉ: San José, *Pittier 14104* (CM, GH, U, US). EL SALVADOR. Volcán de San Salvador, *Calderón 2345* (F, US). GUATEMALA, SACATEPÉQUEZ: San Rafael, *Donnell Smith 2176* (K, US); Antigua, *Standley 62331* (F). SAN MARCOS: Volcán Tajumulco, *Johnston 1231* (F), *Steyermark 62331* (F). INDIA: Ootacamund, Nilgeri Hills, *Anstead 122* (A), *Koelz 11048* (NA), *Marcovicz in 1927* (LE); Kodaikanal, *Bembower 9* (MO); Madras, Shembayanu, *Sauliers 656* (A). JAMAICA: Cinchona Garden, Blue Mts., *Downes in 1926* (BM), *Harris 7643* (G), *Sporne 213* (CGE), *? 7605* (BM, F, K); vicinity of St. Helen's Gap, St. Andrew, *Maxon & Killip 571* (A, F); near New Haven Gap, *Philipson 914* (BM), *Roever 4574* (MICH); Latimer River, *Seifriz in 1919* (BH). JAVA: Preanger, Pengalengan, *Hochreutiner 1463* (G); Bandang, *Rauh 13* (U). MEXICO, CHIAPAS: Piedracitos, Chamula, *Breedlove 8018* (DS). DISTRITO FEDERAL: Villa Obregón, *Moore 6395* (BH); Coyoacán, *Woronow 2065* (LE). PUEBLA: Huauchinango, *Baldwin 14390* (LL). VERACRUZ: Orizaba, *Botteri 929* (GH, K, LE); Jalacingo, *Dodds 57* (MO); Altotonga, *Foster in 1938* (BH, BM); Santa Ana Atzacana, N of Orizaba, *Rosas 191* (MO); Santa Cruz, Altotonga, *Ventura 1026* (CAS). PORTUGAL: Coimbra, *Rhodes 37-64-126* (BH) RÉUNION: Forêt de Bébour, *Lorence & Cadet 2423* (MO); Cilac, Réserve Matambu, *Lourteig 2455* (MO), *Schlieben 10966* (B, Z). SOVIET UNION: *Leningrad Botanical Garden in 1843* (LE). SRI LANKA: Hadgala Garden, *Marcovicz in 1927* (LE). ST. HELENA: Longs, ridge above Sandy Bay, *Kerr 107* (BM); Diana's Peak, *Salter 38418* (BM). UNITES STATES, CALIFORNIA: Univ. Calif. Botanical Garden, Berkeley, *Hutchison 49.802* (MO, RSA, UC, US); Los Angeles, *McClintock in 1942* (NA).

Unlike most species of sect. *Fuchsia,* which are often scandent with weak stems and branches, *Fuchsia boliviana* is sometimes arborescent and almost always self-supporting. Its most distinctive characters are the elongate, drooping racemes of usually scarlet flowers, the cylindrical ovaries and fruits, the fully

reflexed sepals after anthesis, and the early deciduous, ridged petals. In addition, this species generally has large, long petiolate, softly pubescent leaves that are opposite or ternate and sometimes alternate near the branch tips. It has been widely cultivated and naturalized in many countries of the world since the mid-1800s, but has long been confused in the literature with *F. corymbiflora*. The true *F. corymbiflora* has apparently never been cultivated and is a localized endemic in central Peru that has much finer pubescence than *F. boliviana*. It has strictly opposite, short-petiolate leaves, rounder ovaries, much shorter inflorescences, smooth, persistent petals, and non-reflexed sepals. *Fuchsia boliviana* is distinct and easily recognizable from other species of *Fuchsia,* but it is placed in a species group with *F. corymbiflora, F. mathewsii,* and *F. wurdackii* because of their large, pubescent, mostly opposite or ternate leaves and many-flowered racemes of long flowers with narrow petals. It also resembles *F. furfuracea* in the often ovate leaf shape, long petioles, similar floral dimensions, and dense pubescence.

As discussed in the section on reproductive biology, many populations of *F. boliviana* are largely autogamous. Populations from Venezuela and greenhouse-raised progeny from Bolivia both produced fully fertile fruits when isolated from pollinators. The unusually high degree of autogamy in this species is due to the close proximity of the stigma to the upper staminal whorl in many populations and to the loss or very slight degree of protogyny. The pattern of the latter stages of floral maturation is unique in *F. boliviana*. As the sepals split open and start spreading outwards at anthesis, the upper half of the petals begin to curve outwards. Within a day, the sepals become totally reflexed, and the petals attain their final, spreading-recurved posture. About two days after anthesis, the petals shrivel up and fall off, leaving the erect stamens and style along with the sepals reflexed back against the floral tube. The flowers remain on the plant for another day or two before the entire tube usually dehisces.

In addition to autogamy, vegetative reproduction is common in *F. boliviana,* occurring mostly by sucker growth or rooting from broken or cut stems. These two factors account to a large degree for the widely naturalized distribution of this species. The plants are prized for their very striking, numerous, red flowers in long, drooping racemes that can each last several months, and single seeds are sufficient to start extensive local populations in suitably cool, wet areas. In addition, *F. boliviana* has broader ecological tolerances than most species in the section and can survive short periods of drought and full sunlight.

The native range of *F. boliviana* appears to be centered in cloud forest on the eastern slopes of the Andes in southern Peru and Bolivia, possibly extending into northern Argentina. This conclusion is based on historical information as well as an analysis of the habitats and present-day distribution of the species. The only areas where *F. boliviana* can be said to form an integral part of relatively undisturbed tracts of forest is in southern Peru and Bolivia. Elsewhere, this species is found only close to towns, habitations, or heavily disturbed areas, as is typical of adventives or plants escaped from cultivation. Even in southern Peru, many collections are from cultivated or escaped plants. In Venezuela, the only populations of this species are found in the Cordillera de la Costa, where no other native *Fuchsia* occurs. Plants there grow mostly around the Colonia Tovar, an

old German agricultural colony that has received numerous introductions of plant material from travelers and from the numerous botanists who stayed there, such as Fendler, Moritz, and Pittier. *F. boliviana* is very commonly cultivated in the Sabana de Bogotá in Colombia and elsewhere throughout the mountains of that country, but it is always found near human habitations. The species is not known from Ecuador or northern Peru. In Jamaica, it occurs near old abandoned gardens such as Woodcutter's Gap and the Hill Garden at Cinchona and is undoubtedly naturalized (Adams, 1972 and pers. comm. to P. H. Raven).

According to Vargas (1964), *F. boliviana* was cultivated by the Incas and used as a motif in clay and wood artifacts. It continues to be cultivated today in the Cuzco area. The earliest cultivated plants of *F. boliviana* in Europe were grown from seeds brought from Cuzco, Peru. These seeds were collected by relatives of British nurseryman John Standish, who were traders and probably obtained the seed from garden plants there (Lindley, 1840). Progeny of these plants gave rise to many naturalized populations in other parts of the world. Seeds imported from Bolivia in 1873 were also grown in Europe and used to describe *F. boliviana*.

Several varieties or forms of *F. boliviana* have been described based on differences in floral tube length and degree of pubescence. *F. boliviana* var. *luxurians* was described by Johnston (1925) for plants with floral tubes 5–6 cm long from Venezuela, Central America, and Jamaica. In contrast, most plants from Argentina and Bolivia have much shorter floral tubes 3–4.5 cm long and shorter pubescence. The long-flowered populations generally have a more robust growth form and larger inflorescences. The leaves of the small-flowered Bolivian and Argentinian populations may be narrower in many cases than in naturalized plants, but considerable variation is found both in leaf and in floral tube dimensions. For example, *Kelley 1013* (CM, UC), from Sur Yungas, Bolivia, has some floral tubes 6 cm long and others only 4 cm long. Except for the smaller size of flowers and inflorescences in most southern populations, all of the characteristic floral and vegetative traits of these plants are identical to those of the more robust naturalized populations, and both kinds of plants are diploid.

In Dept. Cuzco, Peru, both robust, long-tubed plants as well as shorter-tubed plants are found. Plants such as *Balls B6715* (BM, K, NA, UC, US), cultivated in Paucartambo, near Cuzco, have floral tubes 5–6 cm long and closely resemble the naturalized populations in northern South America, Central America, and Jamaica. As discussed above, the earliest cultivated plants outside of Peru were from Cuzco, and illustrations in Lindley (1840) and Paxton (1841) appear to be from long-tubed plants. Since cultivation of this species in the Cuzco area dates back to the Incas, it is reasonable to suppose that robust, long-flowered plants were selected for cultivation by the local inhabitants, and these were later discovered by European visitors who sent seeds abroad to give rise to many of the naturalized populations known today. Due to the predominant autogamy of this species, populations with different floral tube lengths or with differences in the length and density of pubescence can easily be maintained. The only cultivated or naturalized populations with short floral tubes 4 cm long or less are from Portugal (*Rhodes 37-64-126*, BH) and some from India. Crosses between long-tubed plants from Colonia Tovar, Venezuela, and short-tubed plants from Dept.

La Paz, Bolivia, were made at Missouri Botanical Garden in 1979. These have given rise to normal, vigorous plants, with intermediate flower size.

A white-tubed variant of *F. boliviana* was described by Harrison (1849) as "*Fuchsia corymbiflora alba*." It has also been collected in Colombia (*Berry 3552*, COL, MO; Dept. Tolima) and is characterized by a total loss of red pigmentation in all parts of the plant except the petals. This might be due to a single mutation and is only known in cultivated or naturalized plants.

In summary, *F. boliviana* is a well demarcated species with populations that differ in floral tube length, robustness of the plant, and degree of pubescence. These differences can be explained, however, by a fairly wide and sometimes continuous variation within local populations, a long history of cultivation and probable selection of long-flowered forms, and a high degree of autogamy, which helps maintain small morphological differences. It is a very handsome species that is widely naturalized throughout the world in moist tropical and subtropical, montane habitats, but its probable native range extends from southern Peru (Dept. Apurimac of Cuzco) to Bolivia or northern Argentina. It is known to grow sympatrically with *F. sanctae-rosae* in Peru and Bolivia, but no hybrids between these two species have been detected.

50. Fuchsia corymbiflora Ruiz & Pavón, Fl. Peruv. Chil. 3:87, *pl. 25, fig. a.* 1802. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):551. 1941, pro parte. Munz, Proc. Calif. Acad. Sci. IV. 25:49, *pl. 7, fig. 38.* 1943, pro parte, non auct. pro *F. boliviana*. TYPE: Peru, Dept. Huánuco, woods of Chinchao and Muña, 1778–1788, *Hipólito Ruiz and José Pavón* (MA N°11/78, lectotype, here designated; photograph, MO).

Fuchsia velutina I. M. Johnston, Contr. Gray Herb. 75:36. 1925. TYPE: Peru, Dept. Huánuco, Yanano, ca. 2,000 m, 13–16 May 1923, *J. Francis Macbride 3715* (F 535777, holotype; fragment, G; photographs, NY, POM, UC; GH, K, isotypes).

Fuchsia munzii J. F. Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4):559. 1941. TYPE: Peru, Dept. Junín, Río Masamerich, 2,100–2,200 m, 1909–1914, *August Weberbauer 6648* (F 628941, holotype; photographs, NY, UC; GH, UC, isotypes).

Scandent to erect shrubs 1–4 m tall. Young growth finely canescent to puberulent; older stems and leaves velutinous to subglabrous; branches few and spreading, branchlets terete, 2–3 mm thick, red to dull purple. Leaves opposite, very rarely ternate, firmly membranous, elliptic to oblong, acute at the base, acute to acuminate at the apex, 6–12(–19) cm long, 3–6(–9) cm wide, matte green above, pale green below; secondary veins 13–17 on either side of the midvein, sometimes reddish below; margin subentire to obscurely glandular-denticulate. Petioles 6–20(–30) mm long. Stipules triangular, 1–2 mm long, ca. 1.5 mm wide, sometimes connate, deciduous. Flowers few to many in terminal, corymbose, arching to drooping racemes or few-branched panicles; rachis 2–8 cm long; bracts lanceolate, 5–15 mm long. Pedicels pendant to ascending in fruit, 6–15 mm long. Ovary ellipsoid, 5–6 mm long, ca. 2 mm thick, puberulent. Floral tube narrowly funnelform, 40–65(–70) mm long, 2–2.5 mm wide and bulbous at the base, narrowed to 1.5–2 mm wide for ca. the basal 10 mm of the tube, then gradually widened above until 5–8 mm wide at the rim, minutely pubescent under a lens

to velutinous or strigillose outside, pubescent inside for most of length. Sepals lance-oblong, 12–15 mm long, 3.5–5 mm wide, acute at the apex, buds terete and slightly mucronate, spreading-divergent at anthesis. Tube and sepals pale pink to bright scarlet. Petals darker, red, oblong, acute to obtuse-tipped, 12–17 mm long, 4–5 mm wide, spreading and equal to or longer than the sepals at anthesis. Nectary shallowly 4-lobed, ca. 1.5 mm high. Filaments pink to red, 8–10 mm and 5–7 mm long; anthers oblong, 2.5–3 mm long, ca. 1.5 mm wide, white. Style pink, puberulent from the base to the rim of the tube; stigma capitate, 4-cleft at the apex, 2–2.5 mm long, ca. 2.5 mm wide, cream, exserted 3–6 mm beyond the anthers. Berry subglobose, ± tetragonous before maturity, 10–12 mm long, 8–10 mm thick, red; seeds reddish tan, 1.8–2.1 mm long, 1–1.4 mm wide. Gametic chromosome number $n = 11$.

Distribution: Endemic to cloud forest on the eastern slopes of the central Peruvian Andes in Depts. Huánuco, Junín, and Huancavelica; (1,500–)2,250–2,850 m (Fig. 63).

Representative specimens examined: PERU, HUANCAVELICA: without locality, *Weberbauer 6565* (F, GH). HUÁNUCO: near Panao, above La Molina, *Asplund 13699* (RSA); 5 km W of Carpish tunnel, *Berry & Aronson 3082* (MO, USM); Carpish, *Ferreyra 1828* (MO, USM); Carpish, above Acomayo, *Hutchison et al. 5919* (F, MO, NY, RSA, UC, US, USM); Huacachi, near Muña, *Macbride 4180* (F, G); road from Mirador to Chinchao, *Mexia 7765* (GH, K, MO, UC, US); Muña, *Pearce 148* (K), *512* (BM, K). JUNÍN: 55 km above and W of Satipo on road to Concepción, *Berry & Aronson 3079* (MO, USM); San Juan to Huacapistana, *Ferreyra 11293* (USM); above Huacapistana, *Sandeman 95* (BM, K); Km 170 Satipo-Concepción, *Seibert 2384* (MO, POM, US). WITHOUT LOCALITY: *Ruiz & Pavón* (BM, F, MA, MO).

This species can be recognized by its normally soft, velutinous, opposite leaves and terminal racemes of slender flowers with short pedicels and round fruits. These characters place it in the *Fuchsia boliviana* species group, where it is possibly most closely related to *F. wurdackii* from northern Peru. For over a century its name was used for the species later described as *F. boliviana*, a commonly cultivated and naturalized, ornamental plant from southern Peru and Bolivia that has cylindrical fruits, flowers with reflexed sepals and much longer racemes. Munz (1943) also included *F. dependens* under this species, but it is distinct and restricted to northern Ecuador and southern Colombia and has quaternate, longer petiolate leaves with more toothed margins.

Plants from the southern part of the range in Junín have been called *Fuchsia munzii*. They have much paler pink flowers than populations from Huánuco, and their leaves are lighter green with wine purple veins. This appears to be due to the loss of some of the dark red pigmentation in the plant. Although the Junín plants are often nearly glabrous, the characteristic fine, erect hairs of *F. corymbiflora* can usually be seen upon careful examination. They also have the same 4-sulcate, rounded fruits and finely pilose styles as *F. corymbiflora*. In the Carpish area, considerable variation in leaf width occurs.

Fuchsia corymbiflora is sympatric with *F. abrupta, F. ceracea, F. decussata,* and *F. denticulata*. *Fuchsia abrupta* is a long-tubed species with opposite leaves that can be confused with *F. corymbiflora* in dried specimens, but it can be distinguished by its cylindrical fruits, divergent pedicels, often hispid pubescence, and strongly divergent sepals and petals.

51. Fuchsia wurdackii Munz, Brittonia 16:229. 1964. TYPE: Peru, Dept. Amazonas, Prov. Chachapoyas, Quebrada Molino, 5 km below Chachapoyas, 2,200 m, 30 May 1962, *John J. Wurdack 622* (US 2404206, holotype; photograph, MO).

Erect shrubs 1–1.5 m tall. Young growth finely pilose, older stems pilose and dull tan, 3–10 mm thick. Leaves opposite or ternate, softly membranous, narrowly elliptic-ovate, acute to subacuminate at both ends, 7–18 cm long, 2–8 cm wide, shortly soft pilose on both sides; secondary veins 7–14 on either side of the midvein; margin subdenticulate. Petioles pilose, 7–43 mm long. Stipules conspicuous, lanceolate, usually with an obtuse apex, pale membranous, 3–5 mm long, 0.5–2 mm wide, sometimes connate, usually persistent and reflexed. Flowers few to many in terminal, corymbose, drooping racemes; rachis 4–18 cm long; bracts lance-linear, denticulate, 15–50 mm long, 3–8 mm wide. Pedicels 9–11(–25) mm long. Ovary oblong, 7–10 mm long, 3–4 mm thick. Floral tube narrowly funnelform, 31–50 mm long, 2–3 mm wide and slightly bulbous at the base, gradually widened above until 5–8 mm wide at the rim, pilose to short villous outside, pilose inside in lower ⅔. Sepals oblong, obtuse, 9–16 mm long, 3–5 mm wide, spreading at anthesis. Tube and sepals coral red. Petals red, oblong to broadly elliptic, obtuse at the apex, 11–20 mm long, 4–8 mm wide. Nectary unlobed or shallowly 4-lobed, ca. 1.5 mm high. Filaments red, 5–9 mm and 3–6 mm long; anthers oblong, 2–2.5 mm long, ca. 1.5 mm wide, white. Style red, glabrous; stigma capitate, shortly 4-lobed at the apex, 2–3 mm long, 2–4 mm wide, pink, exserted 1–3 mm beyond the anthers. Berry cylindric to ellipsoid, 17–20 mm long, 9–11 mm thick; seeds 1.6–2 mm long, 0.9–1.2 mm wide. Gametic chromosome number $n = 11$.

Distribution: Northern Peru. Endemic to moist sites on slopes leading into the Río Utcubamba valley in Dept. Amazonas; 2,100–2,400 m (Fig. 63).

Representative specimens examined: PERU, AMAZONAS: 9 km above Leimebamba on road to Balsas, *Berry & Escobar 3616* (MO, USM): Leimebamba-La Joya trail, *Boeke 1786* (MO); Cerros Calla-Calla, at San Miguel, 5 km above Leimebamba, *Hutchison & Bennett 4542* (UC, USM), *Hutchison & Wright 4884* (UC); vicinity of Leimebamba, upstream along creek leading into Río Utcubamba, *Hutchison & Wright 4888* (F, MICH, MO, NY, RSA, UC, US, USM); Cerro Puma Urco, SE of Chachapoyas, *Soukup 4097* (US).

This is a long-tubed, racemosely flowered species that is distinctive in its obtuse petals and sepals, pilose pubescence, and large, pale stipules. Its rather long inflorescences with narrow bracts are similar to those of *Fuchsia pilosa*, but that species has much smaller flowers and coarser pubescence. *Fuchsia wurdackii* shares many features with *F. boliviana* including the large, pubescent, long-petiolate leaves and lanceolate bracts, but lacks the acute, reflexed sepals and long, cylindrical fruits of that species. Its closest relative is probably *F. corymbiflora*, known from central Peru, which has similar flowers and short, soft pubescence, but shorter fruits and petioles. Since *F. wurdackii* is the lowest-altitude species in northern Peru, it does not occur sympatrically with any other species of the section, although both *F. fontinalis* and *F. mathewsii* occur nearby (Fig. 10).

52. Fuchsia mathewsii J. F. Macbride, Candollea 8:24. 1940; Field Mus. Nat. Hist., Bot. Ser. 13(4):558. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:44. 1943. TYPE: Peru, Dept. Amazonas, Chachapoyas, 1830–1841, *Andrew Mathews* (G-BOIS, holotype; photograph, MO; G-DEL, isotype).

Fuchsia fischeri J. F. Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4):554. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:45. 1943. TYPE: Peru, Dept. Cajamarca, Prov. Hualgayoc, Chugar, 2,700–2,900 m, 1906, *August Weberbauer 4097* (G, holotype).

Fuchsia storkii Munz, Proc. Calif. Acad. Sci. IV. 25:37, *pl. 6, fig. 33.* 1943. TYPE: Peru. Dept. Cajamarca, Prov. Chota, pass S of Conchán, 2,500 m, *Harvey E. Stork & Ovid B. Horton 10073* (F 1052248, holotype; photograph, NY; K, UC, isotypes).

Suberect shrubs 1–3 m tall, puberulent to mostly densely pilose with white to generally rusty hairs. Branchlets triangular (when leaves are ternate) or rarely subtetragonous, dull purple to ferrugineous-pilose; older branches 7–14 mm thick, with pilose, reddish bark exfoliating in strips. Leaves mostly ternate, occasionally quaternate, firmly membranous, narrowly elliptic to oblanceolate or elliptic, at times slightly asymmetrical and curved to one side, narrowly obtuse at the base, acute at the apex, 4–16 cm long, 1.2–5 cm wide, dull to subnitid dark green and pilose to strigose above, lighter green and mostly rusty-pilose below, with hairs denser along the nerves, blades sometimes purple flushed; secondary veins 8–12 on either side of the midvein; margin subdenticulate. Petioles pubescent to densely ferrugineous-pilose, 3–10(–25) mm long. Stipules narrowly lanceolate when young, becoming thick and triangular with age, dark, 2–3 mm long, ca. 1 mm wide, subpersistent. Flowers numerous and crowded at the tips of terminal, arching-drooping racemes or few-branched panicles; rachis 3–6 cm long; bracts lacking or rapidly deciduous, 10–25 mm long, ca. 6 mm wide. Pedicels pubescent to pilose, 12–25 mm long. Ovary ellipsoid, 5–7 mm long, 2–3.5 mm thick, green to purple. Floral tube narrowly funnelform, (32–)36–63 mm long, 2.5–3.5 mm wide and slightly bulbous at the base, narrowed to ca. 2 mm wide above the nectary, then widened gradually above until 5–8 mm wide at the rim, mostly pilose outside, pilose to villous inside in lower ½. Sepals lanceolate, blunt tipped and broader than the tube in bud, 11–16 mm long, 4–5 mm wide, lobes often splitting open in the middle before detaching at the tips, suberect to spreading at anthesis. Tube and sepals pale pink to lavender or light red. Petals slightly darker than the tube or sepals, crimson to light purple, lanceolate to narrowly elliptic, 10–16 mm long, 3–4 mm wide, obtuse to subacuminate at the apex, spreading at anthesis. Nectary unlobed, ca. 1.5 mm high. Filaments dull white to light red, 7–9 mm and 4–6 mm long; anthers oblong, 2–2.5 mm long, ca. 1.5 mm wide, white. Style pink, villous from the base to the rim of the tube; stigma subglobose, 4-cleft at the apex, 2.5–3.5 mm long, 2–3 mm wide, pink. Berry subglobose to ellipsoid, 10–16(–20) mm long, 8–11(–15) mm thick, lustrous red purple; seeds 1.8–2.1 mm long, ca. 1 mm wide. Gametic chromosome number $n = 11$.

Distribution: Northern Peru. Scattered to locally frequent shrubs in cloud forest along streamsides or in semidisturbed sites such as roadbanks or thickets, or in somewhat drier, shrubby woodlands; Depts. Cajamarca and Amazonas; (2,500–)2,700–3,350 m (Fig. 63).

Representative specimens examined: PERU, AMAZONAS: 42 km E of Balsas on road to Leimebamba, *Berry & Escobar 3603* (MO, USM); 51 km E of Balsas on road to Leimebamba, *Berry & Escobar 3606* (MO); 24 km above Leimebamba on road to Balsas, *Berry & Escobar 3612* (MO); Prov. Chachapoyas, *Mathews 2112* (K), *s.n.* (BM, K, OXF); above Colcamar, *Pennell 15620* (PH). CAJAMARCA: 39 km W of Celendín on road to Cajamarca, *Berry & Escobar 3602* (MO, USM); canyon of Río Marañón above Balsas, 5 km below summit of road to Celendín, *Hutchison & Wright 5356* (F, NY, RSA, UC, USM); E of Cordillera de Cumulloa to Celendín, *Pennell 15158* (PH, USM).

The generally rusty-pilose pubescence, mostly oblanceolate, ternate, short-petiolate leaves, and the short, nodding inflorescences of long-tubed, pinkish flowers characterize this species. It is somewhat intermediate between the *Fuchsia boliviana* and the *F. dependens* species groups and apparently has no close relative, but it is placed in the former group because of the mostly racemose flowers and generally ternate leaves. *Fuchsia mathewsii* is quite common on the Cerros de Calla-Calla in Dept. Amazonas, occurring on both the western slopes above the dry Marañón valley and on the moister, eastern slopes. Considerable variation in the length and redness of pubescence exists within these populations, and the plants on the western side tend to have somewhat longer petioles than those on the eastern, Leimebamba side. There is just a short distance, ca. 20 km by air, between the populations on the east side of the arid Río Marañón valley in Dept. Amazonas and those on the opposite slopes in Dept. Cajamarca, and the differences between them are no greater than the variation found locally on the Amazonas side. The two species described from areas farther north in Cajamarca, *F. fischeri* and *F. storkii,* show no significant differentiation from the populations described above. *Fuchsia storkii* is supposedly distinguished by its short (30 mm long) flowers, but the type at F examined by Munz proves to have only young flowers; fully extended flowers on the isotype at K have floral tubes up to 48 mm long, well within the normal range for *F. mathewsii.*

Fuchsia fontinalis often has rusty-pilose pubescence and paniculate inflorescences like *F. mathewsii,* but the rachis is more extended and the flowers shorter. Whereas *F. mathewsii* occurs on both sides of the north-south running Cerros de Calla-Calla (between the Marañón and Utcubamba river valleys), *F. fontinalis* grows only on the eastern slopes. There, the two species are sympatric between 3,200 and 3,300 m, at the lower altitudinal limit of *F. fontinalis* and the upper limit of *F. mathewsii* (Fig. 10). They were found growing together in low woods along a pasture border, and a probable hybrid between them was collected growing out of a stone wall nearby (*Berry & Escobar 3613,* MO, USM: 3,260 m, 15 July 1979). This individual has intermediate floral tube lengths (22–32 mm), short, but bracteate inflorescences, and reduced pollen stainability of 36.6% of 500 grains. Another possible hybrid or backcross to *F. mathewsii* is *Berry & Escobar 3611* (MO), found 1 km above *3613*; it is much closer to *F. mathewsii,* with floral tubes ca. 36 mm long, but the style is glabrous, and the inflorescence is bracteate and nearly 12 cm long, as in *F. fontinalis*. Its pollen stainability is also low, 46.6% of 500 grains.

53. Fuchsia dependens Hooker, Ic. Pl. *t. 65.* 1837. TYPE: Ecuador, Prov. Pichincha, woods on W side of Volcán Pichincha, 1838, *William Jameson 81* (K, holotype; photograph, MO).

Fuchsia corymbiflora sensu J. F. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):551. 1941, pro parte; sensu Munz, Proc. Calif. Acad. Sci. IV. 25:49. 1943, pro parte; Opera Bot., Ser. B, 3:13. 1974, pro parte.

Erect to usually scandent-climbing shrubs 2–10 m high, with arching to hanging branches 0.5–3 m long. Branchlets canescent, dull red, 2–8 mm thick, with tan bark exfoliating in longitudinal strips. Leaves mostly quaternate, rarely in whorls of 3 or 5, membranous, narrowly elliptic to ovate, acute at both ends, 5–14(–15) cm long, 2–5(–6) cm wide, dull green and strigillose above, incanous and paler below, especially when dry; secondary veins 11–14(–16) on either side of the midvein, ± impressed above and prominent below, midrib reddish; margin usually undulate and conspicuously glandular-denticulate. Petioles puberulent, reddish, $^1/_5$–⅓ the length of the blade, 14–35 mm long. Stipules lanceolate, 1.5–2 mm long, 0.4–0.5 mm wide, deciduous. Flowers numerous in dense, drooping, terminal panicles or series of terminal and subterminal, corymbiform racemes; rachis 2–6 cm long when young, 8–25 cm long in fruit; bracts elliptic, 5–20 mm long, 3–10 mm wide, short-petiolate, sometimes reflexed. Pedicels slender, pendant, incanous, 5–10 mm long. Ovary ellipsoid, 5–7 mm long, 2–3 mm thick. Floral tube narrowly funnelform or subcylindric, 40–50 mm long, 3–4 mm wide and nodose at the base, narrowed to 2.5–3 mm wide in basal ¼, then gradually widened above until 5–8 mm wide at the rim, puberulent outside, densely pilose inside in the narrowed part of the tube. Sepals lance-oblong, 12–13 mm long, 4–5 mm wide, obtuse to shortly acute-tipped, spreading at anthesis. Tube orange red to scarlet, sepals same but with dull green tips. Petals orange red, narrowly lanceolate, 12–14 mm long, 3–4 mm wide, acute at the apex, spreading to ± recurved at anthesis. Nectary irregularly 4-lobed, 1–2 mm high. Filaments red, 9–11 mm and 5–7 mm long; anthers oblong, 2.5–3 mm long, 1.5–2 mm wide, cream. Style totally glabrous, light red; stigma capitate to subobconic, slightly 4-parted at the apex, 2–2.5 mm long, 1.5–2 mm wide, dull pink, exserted 3–10 mm beyond the anthers. Berry ellipsoid, puberulent, 12–16 mm long, 7–12 mm thick; seeds tan brown, 1–1.2 mm long, ca. 0.6 mm wide. Gametic chromosome number $n = 11$.

Distribution: Southern Colombia to central Ecuador. In cloud forest on the west slopes of the Cordillera Occidental of the Northern Andes from Carchi to Pichincha and on the east slopes of the Cordillera Central in Imbabura and Carchi; also in the drier Central Valley of Ecuador from Pichincha to Carchi and in the Nudo de Pasto area in Nariño, Colombia, occurring commonly in hedgerows; 2,400–3,300 m (Fig. 66).

Representative specimens examined: COLOMBIA, NARIÑO: between pasto and Río Bobo, *Barclay 4645* (COL); 8 km S of Pasto towards Ipiales, *Berry 3145* (MO); Oscurana, S slopes of Volcán Gualcalá, 14 km from Piedrancha, *Fosberg 21186* (RSA, US); Laguna La Cocha, Páramo el Tábano, *García-Barriga 7822* (COL, US); Volcán Galeras, near Pasto, *Lehmann 5497* (F, GH, K, S, US); road from Cuatro Esquinas to Quitasol, *Mora 290* (COL); region of Pedregal, S of Yacuanquer, *Schultes & Villarreal 7898* (COL, RSA); base of Volcán Galeras, above Obonuco, *Schultes & Villarreal 8042* (COL, GH, RSA). ECUADOR, CARCHI: between Paja Blanca and El Cucho, *Acosta Solis 10476* (F); Guaca, San Gabriel, *Balls 7344* (BM, K, MO, NA, UC, US); El Angel, *Berry & Berry 2560* (MO); 38 km W of Tufiño on road to Maldonado, *Berry 3148* (MO); ca. 4 km W of El Carmelo, *Berry 3164* (MO, QCA); town of J. Andrade, on Panamerican highway, *Berry 3166* (MO, QCA).

IMBABURA: Rosaspampa, E slopes of Volcán Mojanda, *Acosta Solis 8089* (F); 4–5 km W of Otavalo to Laguna de Mojanda, *Berry & Berry 2552* (MO), *Berry 3172* (MO, QCA); Mojanda, ca. 10 km SSW of Otavalo, *Sparre 13480* (S). PICHINCHA: San José de Minas, *Benoist 3961* (P); 19 km W of Cotocollao on road to Nanegal, *Berry & Escobar 3176* (MO, QCA); 10 km E of Cayambe, *Harling 4343* (NY, S); between Calacati and Nono, *Hartweg 986* (BREM, CGE, G, K, LE, NY, OXF, P, W); Hacienda Yunguilla, NW of Calacati, *Haught 3170* (A, BH, U); Pululahua Crater, ca. 22 km N of Quito, *Humbles 6281* (AAU, NY); between Cotocollao and Nono, *Mexia 7658* (BM, GH, K, MO, NY, POM, S, U, UC, US); Volcán Pichincha, *Spruce 5471* (BM, CGE, G, K, NY, OXF, TCD, W).

This species is part of a group with mostly quaternate leaves and paniculate inflorescences. Both Munz (1943) and Macbride (1941) treated this species under *Fuchsia corymbiflora*, but that is a distinct species from central Peru with entirely opposite leaves and usually racemose inflorescences. *Fuchsia dependens* is closely related to *F. hartwegii*, with shorter flowers, and to *F. hirtella*, which has more entire leaves with short petioles. Both these species occur north of the range of *F. dependens* in Colombia. It is further distinguished by its densely cinereous pubescence and long-petiolate leaves with conspicuously denticulate and sometimes undulate margins.

Fuchsia dependens has wide ecological tolerances for sect. *Fuchsia*. On the eastern slopes of the Cordillera Central in Ecuador and on the western slopes of the Cordillera Occidental, it is found in cloud forest and occurs mostly as a climber or scrambling shrub. It also occurs in the drier Central Valley of Ecuador and in the Nudo de Pasto in southern Colombia, where it grows more compactly and often as upright shrubs in hedgerows. This is an excellent example of this upland area being used as a migration corridor for a species to spread from one structural unit of the Andes to another. Other species that occur sympatrically with *F. dependens* are *F. ampliata*, *F. corollata*, and *F. sessilifolia*, but no hybrids were detected with them.

54. Fuchsia hirtella Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 6:107. 1823. Munz, Proc. Calif. Acad. Sci. IV. 25:47, *pl. 7, fig. 36*. 1943. TYPE: Colombia, Dept. Cundinamarca, in mountains near Fusagasugá, ca. 1,900 m, July–Sept. 1801, *Alexander von Humboldt & Aimé Bonpland* (P, holotype; photograph, F; microfiche, MO). *Bonpland 1783* at P is a possible isotype.

Climbing-scandent to suberect shrubs 2–5 m tall. Branchlets subterete, 2–4 mm thick, green to reddish and densely hirtellous; older branches 10–25 mm thick, with freely exfoliating bark. Leaves mostly quaternate, occasionally in whorls of 3 or 5, membranous, elliptic to narrowly elliptic or obovate, acute to truncate at the base, acute at the apex, 6–13 cm long, 1.8–5 cm wide, subnitid dark green and loosely strigose above, pale green and densely strigose below; secondary veins 10–15 on either side of the midvein, prominent below; margin entire to subdenticulate. Petioles strigose, reddish, 3–8(–15) mm long. Stipules lance-linear, hirtellous, 1.5–2 mm long, ca. 0.5 mm wide, deciduous. Inflorescence an arching to pendant panicle at the tips of branches; flowers numerous, subtended by reduced, sometimes reflexed leaves; rachis hirtellous, 4–20 cm long. Pedicels slender, pubescent, 4–12 mm long. Ovary cylindric, 5–7 mm long, ca. 2 mm thick. Floral tube subcylindric, 34–40 mm long, 3–4 mm wide and bulbous at the base, narrowed to 2–3 mm wide in the basal ⅓, then gradually widened above until 5–9 mm wide at the rim, strigillose to pilose outside, densely villous

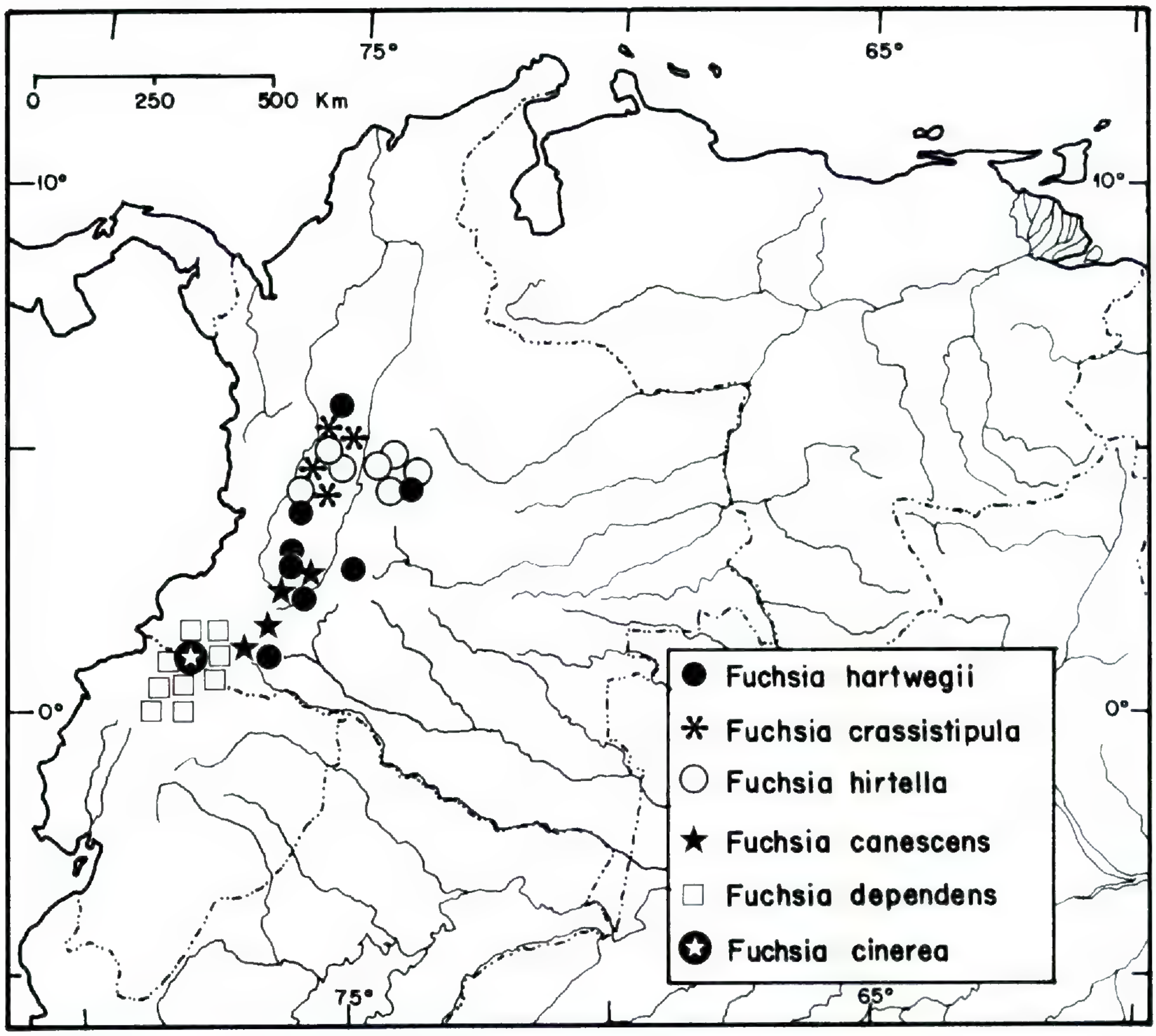


FIGURE 66. Distribution of the *Fuchsia dependens* species group.

inside in basal ½. Sepals lanceolate, acuminate, 12–16 mm long, 3–4 mm wide, long-tapered to apiculate in bud, spreading to divergent at anthesis. Tube and sepals subnitid lavender to reddish pink. Petals somewhat darker, crimson, narrowly elliptic-oblong, sharply acute at the apex, 12–16 mm long, 3–4 mm wide, spreading at anthesis. Nectary unlobed, light green, ca. 1.5 mm high and ca. 1 mm thick. Filaments pink, 8–14 mm and 5–10 mm long; anthers oblong, 2.5–3 mm long, 1.5–2 mm wide, dull white. Style slender, glabrous, pink; stigma globose to subobconic, 4-parted apically, 2–2.5 mm long, ca. 2 mm wide, pale pink to dull red, exserted 3–9 mm beyond the anthers. Berry cylindric-ellipsoid, 14–18 mm long, 8–9 mm thick; seeds 1.4–1.7 mm long, ca. 0.7 mm wide. Gametic chromosome number $n = 11$.

Distribution: Colombia. In the Cordillera Oriental in Cundinamarca, mostly on the outer slopes of the Sabana de Bogotá; in the Cordillera Central from Caldas to Valle; growing in moist cloud forest clearings or thickets between 2,500 and 3,300 m (Fig. 66).

Representative specimens examined: COLOMBIA, CUNDINAMARCA: San Miguel, Km 35–36 S of Sibaté to Fusagasugá, *Barclay et al. 3403* (COL, US), *Berry 3543* (COL, MO); Páramo de Sumapaz, near

Lagunitas, ca. 5 km SSW of San Juan, *Cleef 8451* (COL, MO, U, US); Boca de Monte, *Cuatrecasas et al. 25856* (COL); San Miguel, *Cuatrecasas & Jaramillo 12011* (BH, COL, F, US); Fómeque, between Lago de Chingaza and Cerro Verde, *García-Barriga 17676* (COL); Zipaquirá-Pacho highway, *Haught 5977* (COL, NY, POM, US); La Vega, road to Facatativá, Río Sabaneta, *Schneider 1206* (COL, S); Bojacá, *Schneider 1263* (S); Zipacón, below Boca de Monte, *Uribe-Uribe & Villarreal 2560* (COL, US); 14 km S of Mosquera to La Mesa, *Uribe-Uribe 5929* (COL, US). QUINDÍO: 12 km from Salento towards Cocora, along Río Quindío, *Escobar 1016* (MO); Amarguras, above Salento towards Romerales, *Hawkes 418* (COL, K, US); Laguneta to Magaña, old Quindío trail, *Killip & Hazen 9418* (GH, NY, PH, US). RISARALDA: Guayabal, watershed of the Río Otún, below El Bosque, *Cuatrecasas 23306* (F, RSA, VALLE). TOLIMA: Mediación, *André 2152* (K, NY); 3 km E of La Línea, between Giradot and Armenia, *Berry 3144* (MO); between El Líbano and Murillo, *García-Barriga 12274* (COL, US); La Lora to Cucarronera, new Quindío trail, *Hazen 9679* (GH); Volcancitos, *Holton 893* (K, NY, PH); Tochecito, *Triana 3809* (G, US).

This species is closely allied to *Fuchsia hartwegii* and *F. dependens,* which share a similar paniculate inflorescence and quaternate, pubescent leaves. It can be distinguished from these, however, by its subsessile or shortly petiolate leaves, hirtellous pubescence, and pinkish flowers. Its flowers are longer than those of *F. hartwegii,* which it apparently overlaps in range in the Cordillera Central.

This is a relatively high elevation cloud forest species and is common along the moist, outer slopes of the Sabana de Bogotá. As with *Fuchsia venusta* and *F. petiolaris,* it also grows adjacent to Cundinamarca in Tolima, in the Cordillera Central, where it probably spread secondarily. At its lower altitudinal limit, *F. hirtella* is sympatric with *F. venusta* and *F. verrucosa.* Probable hybrids with *F. venusta* were found between 2,500 and 2,600 m on the southeastern edge of the Sabana de Bogotá in Cundinamarca, where both species are locally common and grow in identical habitats. Table 17 shows the intermediate morphological characters of the two putative hybrids collected. Pollen stainability of these plants was reduced by 18 to 28% relative to their presumed parents (see Table 18). Normal pairing of 11 bivalents was found in meiotic preparations of *Berry 3547* (COL, MO), but occasional chromosomal bridges and fragments were observed at anaphase I.

55. Fuchsia hartwegii Bentham, Pl. Hartw. 179. 1845. Munz, Proc. Calif. Acad. Sci. IV. 25:63, *pl. 9, fig. 53.* 1943. TYPE: Colombia, Dept. Cauca, in woods near Pitayo and Huambía, common in hedgerows at Huambía, 1841–1843, *Theodor Hartweg 994* (K Bentham Herb., holotype; photograph, MO; BM, BR, BREM, CGE, G, K Hooker Herb., LE, OXF, P, W, isotypes).

Low shrubs or small trees 0.5–4 m tall or scandent-climbing in thickets or trees to 8 m above the ground. Young growth usually canescent; branchlets 2–4 mm thick, subterete, reddish, hirtellous to strigose; older branches erect or arching-flexuous on scandent bushes, 0.5–3 m long, 8–50 mm thick, with tan gray, flaking bark. Leaves mostly quaternate, occasionally up to 7 per whorl, firmly membranous, narrowly to rather broadly elliptic or oblanceolate, acute to attenuate at the base, acute to acuminate at the apex, 3–15.5 cm long, 1.5–5.5 cm wide, subnitid dark green and strigose to subglabrous above, pale green and hirtellous to strigose below, especially along the veins; secondary veins 8–14 on either side of the midvein, impressed above, prominent and reddish below; margin glandular-denticulate. Petioles hirtellous to strigose, 5–32 mm long. Stipules lanceolate, thick at the base, filiform at the tip, 1–2 mm long, ca. 0.6 mm wide,

TABLE 17. Comparison of morphological characters of *Fuchsia hirtella*, *F. venusta*, and presumed hybrids.

	F. hirtella (*Berry 3543*)	Hybrid (*Berry 3546*)	Hybrid (*Berry 3547*)	*F. venusta* (*Berry 3544-C, 3547*)
Stem color	Green to pink	Wine red	Wine red	Wine red
Stem pubescence	Hirtellous	Canescent	Canescent	Puberulent
Number of leaves/whorl	4	3–4	3–4	3
Leaf surface	Matte	Subnitid	Subnitid	Nitid
Leaf pubescence	Strigose both sides	Strigose below	Strigose on veins below	Glabrous both sides
Inflorescence type	Paniculate	Subpaniculate	Racemose	Subracemose
Rachis length	13 cm	10–11 cm	5–8 cm	3–4 cm
Pedicel length	9–12 mm	10–25 mm	8–22 mm	16–30 mm
Floral tube length	35–36 mm	35–38 mm	45 mm	30–37 mm
Floral tube color	Pink	Pink purple	Pink purple	Dull orange
Sepal length	12–15 mm	15–18 mm	19 mm	16–20 mm
Sepal angle at anthesis (approx.)	30°	30°	90°	90°
Petal length	12–14 mm	11–14 mm	22–23 mm	16–20 mm
Petal surface	Smooth	Smooth	Undulate	Undulate
Petal color	Pink	Red purple	Red purple	Orange red

deciduous. Flowers hermaphroditic or gynodioecious, numerous, fasciculate, racemose, or more commonly paniculate at the branch tips; rachis 5–20 cm long; bracts broadly ovate, sometimes sessile, 6–20 mm long, 3–15 mm wide. Pedicels slender, arching to pendant, pubescent, 4–12 mm long. Ovary ellipsoid, strigose to pilose, 3.5–5 mm long, 1.5–2 mm thick. Floral tube narrowly funnelform, 13–20(–24) mm long, 1.5–3 mm wide and bulbous at the base, constricted to 1–2 mm wide above the nectary and gradually widened above until 2–5 mm wide at the rim, strigose to pilose outside, densely villous inside in the lower ½–⅓. Sepals lanceolate, 7–12 mm long, 2.5–4 mm wide, acute at the apex, forming a short tip in bud, spreading at anthesis. Tube and sepals subnitid orange red to bright crimson. Petals red, very narrowly elliptic, 5–9 mm long, 1.5–3 mm wide, narrowly acute at the apex. Nectary green, unlobed, 1.5–2 mm high, ca. 0.8 mm thick. Filaments red, 5–8 mm and 3–5 mm long; fertile anthers oblong, 1.5–2 mm long, 0.7–1 mm wide, white, abortive ones ca. ½ as large and nondehiscing. Style glabrous, red; stigma subglobose, barely 4-parted at the apex, 1–1.5 mm long, 1- 1.5 mm wide, pale red, exserted 3–6 mm beyond the anthers. Berry globose when ripe, 6–9 mm long, 5–8 mm thick, nitid purple red; seeds tan to reddish brown, 1.1–1.3 mm long, ca. 0.7 mm wide. Gametic chromosome number $n = 11$.

Distribution: Colombia. Most common in the Cordillera Central from southern Valle to Putumayo, as a scandent or hedgerow shrub in cloud forest between 2,350 and 2,750 m; present farther north in the Cordillera Central around 3,000 m in Caldas, Tolima, and southern Antioquia; a few collections are known from the Cordillera Oriental in Huila and Cundinamarca at 2,100–2,300 m (Fig. 66).

TABLE 18. Pollen stainability of *Fuchsia hirtella*, *F. venusta*, and presumed hybrids.

Collection	Stainable Pollen Grains (% of 500)
Berry 3543 (*F. hirtella*)	95.6%
Berry 3546 (hybrid)	78.4%
Berry 3547 (hybrid)	68.8%
Berry 3544-C (*F. venusta*)	96.2%

Representative specimens examined: COLOMBIA, ANTIOQUIA: Páramo de Sonsón, *Guarín 3479* (COL, US). CALDAS: without locality, *Dawe 741* (K, NY, US); 7 km N of Manizales, *Escobar 1002* (MO); Manizales, *Sandeman 5666* (COL, K, OXF); San Félix, near Salamina, *Tómas 2406* (BH). CAUCA: Puracé, *Alston 8137* (BM, RSA, UC); between Silvia and Totoró, *Berry 3573* (COL, MO); 21 km above Piendamó on road to Silvia, *Berry 3572* (COL, MO); Quebrada Santo Domingo, headwaters of the Río Palo, *Cuatrecasas 19159* (A, BH, COL, VALLE); La Tolda, above Tacueyo, watershed of Río Palo, *Cuatrecasas 19421* (A, BH, VALLE); Puracé, 17 km SE of Popayán, *Fosberg 20303* (COL, RSA, S, US); Río Santo Domingo, 20 km SE of Corinto, *Fosberg 21306* (GH, RSA, S, US); from Puracé to Alto de San Rafael, *García-Barriga & Hawkes 12856* (COL, US); Paispamba, *Haught 5302* (COL, US); Cococnuco, *Killip 6829* (GH, NY, PH, US); Central Andes of Popayán, *Lehmann 5613* (F, K); Páramo de Guanacas, *Lehmann 5614A* (F, GH, K, PH, S, US); Alto de Pesares, *Lehmann 5614B* (F, K); Páramo de Puracé, at Chiquín, *Pérez-Arbelaez & Cuatrecasas 5973* (COL, F, US); between Popayán and Puracé, bridge at Uarló, *Pérez-Arbelaez & Cuatrecasas 5880* (COL, F); headwaters of Río Lopez, Río Palo basin, Tierra Adentro, *Pittier 1068* (US); Prov. of Popayán, *Triana s.n.* (BM); Silvia, Guambía, *Yepes-Agredo 3088* (COL). CUNDINAMARCA: Fómeque, *Dawe 352* (K, US); Río Blanco valley, 6 km W of Gutiérrez, *Grant 9695* (RSA, US); between Guayabetal and Quétame, *Vogel 175* (U). HUILA: ca. 75 km W of La Plata on road to Puracé, *Berry 3591* (COL, MO); headwaters of Río Fortalecillas, just below Paso de Las Cruces, 39 km E of Neiva, *Fosberg 19785* (NY, RSA, S, UC, US); Balsillas, on Río Balsillas, *Rusby & Pennell 789* (NY, US), *810* (NY). META: Río Grande, S of Cordillera de Las Cruces, *Fosberg 20872* (US). PUTUMAYO: above Sibundoy on road to La Cocha, *Berry 3255* (MO, PSO); Balsayaco, valley of Sibundoy, *Bristol 642* (COL, DS, GH); near San Francisco, *Cuatrecasas 11541* (COL, F, US); upper part of Río Minchay, Río Mocoa drainage, *Fosberg 20401* (RSA); Portachuelo, valley of Sibundoy, *Schultes & Villarreal 7725* (COL, RSA, US); Sibundoy, *Schultes & Villarreal 7688* (COL, F, GH, NY, RSA, US). RISARALDA: above Santa Rosa de Cabal, Cháquiro-Páramo de Santa Rosa trail, S of Cháquiro Falls, *St. John 20837* (GH, MICH, US). TOLIMA: 47 km W of Fresno on road to Manizales, *Berry 3557* (COL, MO); La Esperanza, Fresno, *Hanbury-Tracy 624* (K). VALLE: above El Guayabo on Palmira-Taco road, *Berry & Escobar 3568* (COL, MO). Palmira, *Duque-Jaramillo 4699* (COL); above La Magdalena, Buga, *Espinal 2057* (MO).

This species is closely allied to *Fuchsia dependens* and *F. hirtella,* based on their predominantly quaternate leaves and paniculate inflorescences. *Fuchsia hartwegii* is the only species with mostly paniculate inflorescences that has short flowers, very narrow petals, and globose fruits.

The species, as treated here, comprises three main geographical groups that may upon further examination warrant recognition as distinct taxa. The first group, including the type collection, is centered around the moist, western, mid-elevation slopes of the Cordillera Central in Cauca, extending as far north as southern Valle and reaching south to Putumayo on the eastern slopes of the same Cordillera. These populations have orange red flowers and are common in roadside thickets, hedgerows, and along streams, where they sometimes occur as lianas.

A second group is found farther north in the Nevado de Ruiz Massif of the Cordillera Central, in Caldas, Tolima, and Antioquia. These plants differ from the first group in their somewhat smaller, cherry red flowers, short-petiolate leaves, and higher altitudinal range. Of the seven collections known from this area, four are male-sterile, *Berry 3557, Guarín 3479, St. John 20837,* and *Tomás 2406*. Of

the much more numerous collections from the first group to the south, only five male-sterile plants were found, *Haught 5302*, *Lehmann 5613*, *Pittier 1068*, *Schultes & Villarreal 7688*, and *Triana s.n.*

A third group consists of collections from the Cordillera Oriental. *Fosberg 19885* from Huila is very similar to more or less stunted plants that grow in exposed habitats in Cauca, and it is male-sterile. The Cundinamarca collections are all hermaphroditic with mostly fasciculate flowers and differ quite notably from the other groups in having narrow, nearly sessile leaves that resemble those of *F. hirtella*.

Population studies of the different groups discussed above will be required to determine the frequency of male sterility and its relative significance in the breeding system of this species. The finding of male-sterile plants from widely separated localities does suggest that gynodioecy is functioning in at least some populations of *F. hartwegii*. If confirmed, this would be the first report of male sterility in any of the main Andean-Brazilian sections of the genus, which comprise some 75 of the estimated 100 species in *Fuchsia*. Male sterility is presently known only in sects. *Encliandra*, *Kierschlegeria*, *Schufia*, and *Skinnera* (Arroyo & Raven, 1975).

56. Fuchsia crassistipula P. Berry, **sp. nov.** TYPE: Colombia, Dept. Tolima, 40 km W of Fresno on Mariquita-Manizales highway, 2,700 m, 4 June 1979, *Paul E. Berry 3553* (COL 66345, holotype; MO, isotype). Figs. 18, 36.

Frutex erectus vel scandens 1–3 m altus. Ramuli costati, canescenti-strigulosi. Folia 3–6-verticillata plerumque quaterna, firme membranacea, elliptica vel late oblanceolata basi obtusa vel acuta apice acuta vel acuminata, 6–16 cm longa, 2.5–7 cm lata, superne subvelutina atroviridiaque, subtus pallidioria vel purpurascentia sparsim strigosaque; nervis secundariis utroque latere 10–15, margine glanduloso-serrulata et saepe purpurascenti; petiolis validis, 2–3.5 mm crassis, 12–40 mm longis; stipulis persistentibus, conspicuis, saepe connatis, subtriangularibus, patenti-recurvatis, 2.5–4 mm longis, ca. 3 mm latis, costa media 2–3 mm crassa (in vivo), in sicco aliquantum minore. Flores roseo-scarlatini, numerosi in racemis (sub-)terminalibus vel paniculis verticillatim racemosis dispositi; rhachidi costata, nutanti, 5–30 cm longa; bracteis 8–20 mm longis; pedicellis 3–8 mm longis; ovario cylindrico, 5–8 mm longo. Tubi florales anguste infundibuliformes, 32–44(–48) mm longi, basi 3–5 mm lati et subnodosi inde 2–3 mm lati constricti superne gradatim dilatati summo 5–8 mm lati, extus strigulosi intus infra medium pilosi. Sepala lanceolata, acuta, 10–14 mm longa, 4–6 mm lata. Petala rubra vel atrorubra, anguste oblongo-elliptica, acuta, mucronata, 11–16(–18) mm longa, 3–5(–6) mm lata. Filamenta rubra, antisepala 7–11 mm longa, antipetala 4–7 mm longa; antheris oblongis, 2.5–3 mm longis, ca. 1.5 mm latis, albis. Stylus roseus glaberque, stigmate globoso, apice leviter 4-fisso, 3–4 mm longo, 2–3 mm lato, valde roseo-rubro. Bacca cylindrica, in maturitate subglobosa, 13–15 mm longa, 9–13 mm crassa, viridis vel purpurascens; seminibus inaequaliter oblongo-triangularibus, ca. 1.5 mm longi, 0.8–1.1 mm latis. Numerus gameticus chromosomatum $n = 11$.

Suberect to scandent shrubs 1–3 m tall. Young branches conspicuously 3–6-ridged, one ridge for each leaf in the whorl above, 3–9 mm thick, green, strigillose to subcanescent; older branches terete with dull gray brown, exfoliating bark. Leaves 3–6-verticillate, mostly in whorls of 4 or 5, firmly membranous, elliptic to broadly oblanceolate, acute to obtuse at the base, acute to acuminate at the apex, 6–16 cm long, 2.5–7 cm wide, sparsely strigose and velvety dark green above, strigose and paler to purple flushed below, especially on and along the prominent midrib; secondary veins 10–15 on either side of the midvein; margin glandular-serrulate and usually purple tinged. Petioles stout, 2–3.5 mm thick, 12–40 mm long, sparsely strigose, green to pink red. Stipules conspicuous, subtrian-

gular, divergent, margins and tips recurved on lower nodes, separate to fully connate, thick-callose, 2.5–4 mm long and ca. 3 mm wide when fresh, each stipule with a central longitudinal nerve 2–3 mm thick, considerably flattened and shrunken when dry, persistent. Flowers numerous in terminal or subterminal racemes or verticillately branched panicles; rachis ridged, spreading to drooping, 5–30 cm long; bracts 8–20 mm long. Pedicels short, pendant, 3–8 mm long. Ovary cylindrical, 5–8 mm long, 2–4 mm thick, green, strigose. Floral tube narrowly funnelform, 32–46(–48) mm long, 3–5 mm wide and bulbous at the base, narrowed to 2–3 mm wide above the nectary, then gradually widened above until 5–8 mm wide at the rim, finely strigose outside, pilose inside in lower ½. Sepals lanceolate, acute, 10–14 mm long, 4–6 mm wide, with a short tip 1–2 mm long in bud, spreading at anthesis. Tube subnitid scarlet pink; sepals similar but becoming dull purple towards the tip. Petals deeper red, narrowly elliptic-oblong, acute and ± mucronate at the apex, 11–16(–18) mm long, 3–5(–6) mm wide, spreading at anthesis. Nectary green, unlobed, ca. 2 mm high, 0.8–1 mm thick. Filaments 7–11 mm and 4–7 mm long; anthers oblong, 2.5–3 mm long, ca. 1.5 mm wide, white. Style glabrous, pink; stigma globose, 4-parted at the apex, 3–4 mm long, 2–3 mm wide, bright red pink, exserted 3–8 mm beyond the anthers. Berry cylindric to subglobose when fully ripe, 13–15 mm long, 9–13 mm thick, nitid green to flushed purple; seeds ca. 1.5 mm long, 0.8–1.1 mm wide. Gametic chromosome number $n = 11$.

Distribution: Central Colombia. Infrequent shrubs in cloud forest thickets of the Nevado de Ruiz Massif in the Cordillera Central, in Depts. Tolima, Quindío, and Caldas; 2,600–3,000 m (Fig. 66).

Specimens examined: COLOMBIA, ANTIOQUIA: Támesis, vicinity of Medellín (Mislabel?), *Toro 956* (NY). CALDAS: San Félix, near Salamina, *Tomás 2051* (US). QUINDÍO: Salento to Lagunetas, Old Quindío trail, *Killip & Hazen 9141* (GH, NY, PH, US); Penares, above Salento, *Pennell 9195* (GH, PH), *9324* (GH, NY, PH, US). TOLIMA: 43 km W of Fresno on Mariquita-Manizales highway, *Berry 3554* (COL); La Palmilla, Quindío, Mariquita, *Triana 3812* (BM, G, K, P, W).

This species is closely related to *Fuchsia hirtella*, which shares the often paniculate inflorescence, short-cylindrical ovaries, glabrous style, and very similar tube and petal dimensions. *Fuchsia crassistipula* is unique in its strongly ridged stems and thick, persistent stipules. The flowers are also more purple than those of *F. hirtella*. All these characters are usually lost upon drying, however, making it difficult to distinguish between the two species in dried specimens. However, *F. crassistipula* has longer, thicker petioles, more serrulate leaves, and often more than four leaves per whorl. Although *F. crassistipula* occurs in the same area as *F. hirtella*, the two are not known to actually grow together.

57. Fuchsia canescens Bentham, Pl. Hartw. 178. 1845. TYPE: Colombia, Dept. Cauca, near Popayán, ascent to Páramo de Guanacas, 1842, *Theodor Hartweg 992* (K Bentham Herb., holotype; photograph, MO; BREM, K Hooker Herb., isotypes).

Shrubs 1.5–4 m tall. Young branches ridged, the number of ridges the same as the number of leaves in the whorl above, canescent to hirtellous, reddish, 3–8 mm thick; older branches with tan, exfoliating bark. Leaves 3–5-verticillate,

mostly quaternate, firmly membranous, (narrowly) elliptic to (ob-)ovate, acute to rounded at both ends, 4.5–10 cm long, 2–5 cm wide, medium to dark green and strigillose above, hirtellous to densely strigillose and paler below, with the midvein prominent and reddish; secondary veins 8–15 on either side of the midvein; margin subentire to denticulate. Petioles stout, 15–25 mm long, hirtellous, dull purple. Stipules 0.8–1 mm thick when fresh, lingulate to subterete in transection, subulate at the tip, 1.5–2 mm long, ca. 0.8 mm wide, divergent, occasionally connate, hirtellous, subpersistent. Flowers few to many in upper, leafy nodes or in terminal to subterminal, leafy racemes; rachis 2–10 cm long. Pedicels stout, subtuberculate, pendant, hirtellous-canescent, 5–13 mm long, dull green. Ovary cylindrical, subtuberculate, 10–11 mm long, 3–4 mm thick, hirtellous, light green. Floral tube narrowly funnelform, 34–50 mm long, firmly thick-spongy, 1–2 mm thick when fresh, 3.5–5.5 mm wide and slightly bulbous at the base, narrowed to 3–4.5 mm wide above the nectary, then gradually widened above until 5–9 mm wide at the rim, hirtellous and finely striated-tuberculate outside, densely villous inside in the lower ½–⅓. Sepals similarly thick-tuberculate, triangular, 14–18 mm long, 6–9 mm wide, spreading to divergent at anthesis; buds tetragonous in transection, 1–2 mm wider at the base than the rim of the tube and with small protuberances at the base of adjacent sepals, the tip obtuse or shortly pointed. Tube dull scarlet or orange red, sepals becoming dull white or greenish toward the tip. Petals darker red, subtrullate, 14–19 mm long, 4–7 mm wide, margin slightly undulate, spreading to slightly recurved at anthesis. Nectary light green, irregularly 4-lobed, 1.5–2 mm high, ca. 1 mm thick, often with a few erect, stiff hairs on the top. Filaments red, 9–12 mm and 5–8 mm long; anthers oblong, 3–4.5 mm long, 1.5–2 mm wide. Style orange red, glabrous; stigma capitate, 4-parted at the apex, 2.5–3 mm long, ca. 2 mm wide, red to light pink, exserted 4–9 mm beyond the anthers. Berry ellipsoid, 12–15 mm long, 8–10 mm thick, subtuberculate, green to flushed purple; seeds ca. 1.5 mm long, 0.6–0.8 mm wide. Gametic chromosome number $n = 11$.

Distribution: Southern Colombia. Infrequent shrubs in wet subpáramo or upper cloud forest in Cauca, Huila, and Nariño; 2,800–3,350 m (Fig. 66).

Representative specimens examined: COLOMBIA, CAUCA: 31 km E of Totoró on road to Inzá, *Berry 3578* (COL, MO); 34 km E of Totoró to Inzá, *Berry 3579* (MO); 17 km E of Puracé, *Berry 3581* (COL, MO); Km 56 of Totoró-Inzá road, *Escobar 1042* (MO); Páramo de Las Papas, between El Boquerón and La Hoyola, *Idrobo et al. 3918* (COL, P); Paletara to Calaguala, *Pennell 7083* (GH, NY, PH, US), *7094* (GH, NY, PH, US); Canaan, Mt. Puracé, *Pennell & Killip 6669* (GH, NY, PH, US); Las Escaleretas, Moras valley, Río Paez basin, Tierra Adentro, *Pittier 1382* (US); Silvia, Guambía, *Yepes-Agredo 3078* (COL). HUILA: ca. 40 km E of Puracé to La Plata, *Berry 3589* (COL, MO). NARIÑO: 31 km E of Pasto on road to Sibundoy, *Berry 3254* (MO, PSO); Volcán de Sotará, *Lehmann 6194* (COL).

Because of an incorrectly numbered type collection of *Fuchsia corollata* at Geneva, Munz (1943) thought that *F. canescens* was synonymous with that species. Both *Hartweg 992* and *Hartweg 993*, the type collection numbers of *F. canescens* and *F. corollata*, respectively, were collected in the same area, so one of the duplicates may have been easily mislabelled. The holotype of *F. canescens* allows no doubt that it is distinct from *F. corollata*. It has dull orange red flowers with thick, firm walls, somewhat tuberculate ovaries and tubes, short pedicels, trowel-shaped petals, and sepals that are tetragonous in bud. It is a very localized and

rather rare species, found only in high elevation cloud forest and subpáramo elfin forests between Cauca and Nariño, and mostly on the east-facing slopes of the Cordillera Central. Though the thick-tubed flowers are characteristic of the *F. denticulata* species group, the generally quaternate leaves, hirtellous pubescence, and mostly racemose flowers place it closer to the *F. dependens* species group, even though it has no close relative in that group. When dried, specimens of this species are likely to be confused with *F. dependens,* but *F. canescens* has fewer, more axillary flowers, ridged stems, stout pedicels, and hirtellous rather than cinereous pubescence.

Berry 3577-B (MO) and *Escobar 1038* (MO) were both collected on the upper eastern slopes of the Cordillera Central in Cauca, at ca. 3,250 m, ca. 31 km E of Totoró on the road to Inzá. Both appear to be hybrids between *F. canescens* and *F. caucana,* species that have similar tube lengths and grow side by side at this locality. *Escobar 1038* has thick flowers typical of *F. canescens,* but the leaves are subsessile, coriaceous, and elliptic, characters that place it closer to *F. caucana*. Its pollen stainability is less than 15% of 500 grains, and that of *Berry 3577-B* is less than 1%. Throughout their range in the Nudo de Pasto, from Cauca to Nariño, *F. canescens* and *F. caucana* are almost always found growing together or nearby. One collection of *F. canescens* was made on the western slopes of the Cordillera Central above Puracé in Cauca, where it was sympatric with *F. corollata*.

58. Fuchsia cinerea P. Berry, **sp. nov.** TYPE: Ecuador, Prov. Carchi, just E of the town of Tufiño, 3,210 m, 22 Oct. 1978, *Paul E. Berry 3147* (MO 2737070, holotype; QCA, isotype).

Frutex erectus vel scandens 2–5 m altus, ramulis foliisque junioribus dense cinereo-strigulosis. Ramuli angulati, caulibus teretibus. Folia quaterna vel interdum ternata, membranacea, strigulosa, anguste elliptica, basi acuta apice acuta vel obtusa, 2–5(–7) cm longa, 1–2(–3) cm lata, nervis secundariis utroque latere 5–8(–9) subtus saepe rubrescentes, margine subdenticulata; petiolis 5–12(–20) mm longa; stipulis lanceolatis, 1.5–2 mm longis, ca. 0.5 mm latis, deciduis. Flores axillares, dependentes, plerumque 3–4-verticillati; pedicellis (4–)8–20 mm longis; ovario ellipsoideo vel subpyriformi, 5–8 mm longo, dense cinereo. Tubi florales obscure aurantiaci, infundibuliformes, 42–50 mm longi, basi 3–3.5(–4) mm lati et leviter bulvosi inde 2–2.5(–3) mm lati constricti, superne gradatim dilatati summo 5–6(–8) mm lati, extus striguloso-pilosuli, intus pubescentes. Sepala anguste lanceolata, acuta, 15–19 mm longa, 3–4 mm lata, aurantiaca apice viridescentia. Petala aurantiaca vel coccinea, oblonga vel anguste elliptico-lanceolata, 12–15 mm longa, 4–4.5 mm lata. Filamenta antisepala 10–11 mm longa, antipetala 7–8 mm longa; antheris oblongis, eburneis, 2.5–3 mm longis, ca. 1.5 mm latis. Stylus strigulosus usque ad summum tubi, stigmate globoso apice leviter 4-fisso ca. 2 mm longo, 2–3 mm lato. Bacca ellipsoidea, in maturitate subglobosa, cinereo-velutina, ca. 12 mm longa, ca. 10 mm crassa; seminibus inaequaliter oblongo-triangularibus, 1.7–1.8 mm longis, ca. 1 mm crassis. Numerus gameticus chromosomatum $n = 11$.

Erect to scandent shrubs 2–5 m tall. Young growth densely cinereous-strigillose; branchlets angled, 1–2.5 mm thick; older branches terete, with tan bark. Leaves quaternate or less often ternate, membranous, narrowly elliptic, acute at the base, acute to obtuse at the apex, 2–5(–7) cm long, 1–2(–3) cm wide, matte light green and strigillose above, paler and strigillose below; secondary veins 5–8(–9) on either side of the midrib, usually reddish brown; margin subdenticulate. Petioles strigillose, 5–12(–20) mm long. Stipules lanceolate, 1.5–2 mm long, ca. 0.5 mm wide, deciduous. Flowers axillary, pendant, usually in whorls of 3 or 4. Pedicels strigillose, (4–)8–20 mm long. Ovary ellipsoid to subpyriform, 5–8 mm

long, 2–3 mm wide, densely cinereous. Floral tube narrowly funnelform, 42–50 mm long, 3–3.5(–4) mm wide and slightly bulbous at the base, 2–2.5(–3) mm wide above the nectary, then gradually widened above until 5–6(–8) mm wide at the rim, strigillose to pilose outside, pubescent inside. Sepals narrowly lanceolate, 15–19 mm long, 3–4 mm wide, acute at the apex, spreading at anthesis. Tube and sepals dull orange, sepals with dull green tips. Petals orange to crimson, oblong to narrowly elliptic-lanceolate, 12–15 mm long, 4–4.5 mm wide, obtuse to acute at the apex, spreading at anthesis. Nectary 4-lobed, ca. 1.5 mm high. Filaments orange red, 10–11 mm and 7–8 mm long; anthers oblong, 2.5–3 mm long, ca. 1.5 mm wide, cream. Style strigose from the base to near the rim of the tube; stigma globose, slightly 4-lobed at the apex, ca. 2 mm long, 2–3 mm wide, orange red, exserted 4–10 mm beyond the anthers. Berry ellipsoid to subglobose at maturity, canescent to velutinous, ca. 12 mm long, ca. 10 mm thick; seeds 1.7–1.8 mm long, ca. 1 mm wide. Gametic chromosome number $n = 11$.

Distribution: Known only from the base of Volcán Chiles along the Colombian-Ecuadorian border; 3,100–3,250 m (Fig. 66).

Specimens examined: COLOMBIA, NARIÑO: near village of Chiles, *Camp E-340* (NY, RSA, US), *Wiggins 10580* (DS, POM). ECUADOR, WITHOUT LOCALITY: *Lobb 87* (K).

This species is distinguished by its dense, fine, ashy pubescence, angled stems, small, quaternate leaves, and slender, axillary flowers. It is only known from the adjacent villages of Tufiño and Chiles, on opposite sides of the Colombian-Ecuadorian border, where it grows in secondary thickets at the edge of the towns. This area is not heavily forested and is drier than the opposite side of the Cordillera Occidental. The quaternate leaves, fine, ashy pubescence, and floral dimensions are very similar to those of *F. dependens,* which grows nearby, but has flowers grouped in terminal panicles. *Fuchsia vulcanica* is possibly a related axillary-flowered species that grows close by on the slopes of Volcán Chiles, but at higher elevations; it has coarser pubescence and much wider petals.

59. Fuchsia triphylla Linnaeus, Sp. Pl. 1193. 1753. Plumier, Pl. Amer. *pl. 133, fig. 1.* 1757. Hook., Bot. Mag. *t. 6795.* 1885. Duren, Rev. Hort. Belge Etrangère 15:265, *t.* 1889. Watson, Garden (London) 41:32, *pl. 839.* 1892. Bosschère, Ill. Hort. 43:94, *fig. 10.* 1896. Sieb. & Voss. ex Vilm., Blumengart. ed. 3, 1: *t. 84, fig. 336.* 1896. Bailey, Cycl. Amer. Hort. 2:615, *fig. 877.* 1900. Barker & Dardeau, Flore d'Haiti 270. 1930. Essig, Nat. Hort. Mag. 13:1, *fig.,* 15, *photo.* 1934. Munz, Proc. Calif. Acad. Sci. IV. 25:33, *pl. 4, fig. 20.* 1943. Bailey, Stand. Cycl. Hort. 1303, *fig. 1606.* 1963. LECTOTYPE here designated: *Plate 14* in Plumier, Nov. Pl. Amer. Gen. 1703. Linnaeus simply states the locality as "in America," but Lamarck (1788) reports that Plumier found the plant in Haiti "dans des lieux incultes, en allant du quartier de la Bande du Sud à celui qu'on nomme de grand Cul-de-Sac." This locality belongs to the present Département de l'Ouest of Haiti; "la Bande du Sud" probably refers to the southern Massif de la Selle mountain range, and "le grand Cul-de-Sac" is the name of a river originating north of Morne La Visite and flowing northwards, then westwards to Port-of-Prince. Plumier worked in Haiti and Martinique from 1689 to 1697, where he collected objects of natural history and made numerous illustrations of plants. Fig. 29.

Fuchsia racemosa Lamarck, Encycl. 2:565. 1788, nom. illeg. based on *F. triphylla* L.; Tabl. Encycl. *pl. 282, fig. 1, a–h*. 1792. Descourt., Fl. Méd. Antilles 2:161, *pl. 109*. 1822. non Sessé & Moçino, 1888.

Subshrub to low shrub 3–20 dm tall with erect to drooping branches. Young growth canescent to short pilose; branchlets pubescent, reddish; older branches with tan, exfoliating bark. Leaves opposite or ternate, rarely quaternate, firmly membranous, narrowly lanceolate to elliptic or oblanceolate, acute to narrowly cuneate at the base, acute to acuminate at the apex, 2.5–10(–13) cm long, 1–4 (–5.5) cm wide, dull medium to dark green and strigillose above, pale green to commonly flushed metallic purple and strigose below; secondary veins (6–)7–13 on either side of the midvein, mostly impressed above, elevated and often reddish below; margin subentire to finely denticulate. Petioles pubescent, 4–15(–25) mm long. Stipules lance-linear, 1.5–3 mm long, mostly deciduous. Flowers numerous in suberect to mostly nodding, terminal racemes, occasionally subracemose; rachis 4–12(–15) cm long; leaves subtending the flowers mostly reduced, narrowly lanceolate, and deciduous, but similar to normal leaves if flowers subracemose. Pedicels lightly pilose, 10–30 mm long, divergent to nodding. Ovary ellipsoid, 5–7 mm long, 1.5–2.5 mm wide. Floral tube 25–40 mm long, 2–3.5 and bulbous at the base, sometimes with a ring-like inflation of the tube at the base surrounding the nectary, constricted rather strongly to 1–2.5 mm wide in the lower (6–)10–18 mm of the tube, then abruptly dilated to 8–11 mm wide before narrowing slightly towards the rim; pubescent outside, glabrous inside. Sepals lanceolate, 10–13 mm long, 3.5–4.5 mm wide, spreading at anthesis. Tube and sepals orange to coral red. Petals orange to coral red, elliptic-ovate, rounded to broadly acute at the apex, 6–9 mm long, 4–6 mm wide, suberect to spreading at anthesis. Nectary shallowly 8-lobed, ca. 1 mm high. Filaments orange red, 5–7 mm and 3–4 mm long; anthers oblong, ca. 2.5 mm long, ca. 1.5 mm wide, cream. Style orange red, glabrous; stigma capitate, slightly 4-lobed at the apex, ca. 1.5 mm long and wide, pale red. Berry subglobose to ellipsoid, strigose and ± 4-angled before maturity, 15–18 mm long, 11–13 mm thick, glossy red purple when ripe; seeds tan, 1.8–2.1 mm long, ca. 1 mm wide. Gametic chromosome number $n = 22$.

Distribution: Endemic to the island of Hispaniola (West Indies); in Haiti, in the southern Massif de la Hotte and Massif de la Selle, in the central Chaîne des Matheaux, and (rare) in the northern range in the Montaignes Noires and Chaîne de Plaisance. In the Dominican Republic, in the southern Sierra de Baoruco, in the central Sierra de Neiba, and in the northern Cordillera Central. Low shrubs on exposed slopes, moist banks, and edges of pine and mixed pine-broadleaf forest; (700–)1,100–2,000 m (Fig. 67).

Specimens examined: HAITI, ARTIBONITÉ: Massif des Cahos, Montaignes Noires, Petite Rivière de l'Artibonité, Pérodin, ridge above Ingrand, *Ekman 3445* (S). NORD: Citadelle du roi Christophe, on mountain top 5 km SE of Milot, *Bartlett 17380a* (MICH, US). OUEST: Forêt-de-Pins, Massif de la Selle, *Bailey 185* (BH, US); Massif de la Selle, Morne Franchant, *Ekman 1170* (K, S, US); Massif de la Selle, Morne Cabaio, near Jardin Bois Pin, *Ekman 1621* (S); Massif des Matheaux, Grand-Bois, hills towards Toussaint, *Ekman 5706* (S); Massif de la Hotte, eastern group, Grand Goâve, Morne Calumette, *Ekman 7339* (G, S); Massif des Matheaux, l'Arcahaie, Habitation Counolle, *Ekman 9302* (S); Morne des Commissaires, *Holdridge 850* (MICH, US); le Grand Fond de Port-au-Prince, *Jaeger 99* (LE); vicinity of Mission, Fond Verettes, *Leonard 3681* (NY, US), *3701* (NY), *3701a* (US). WITH-

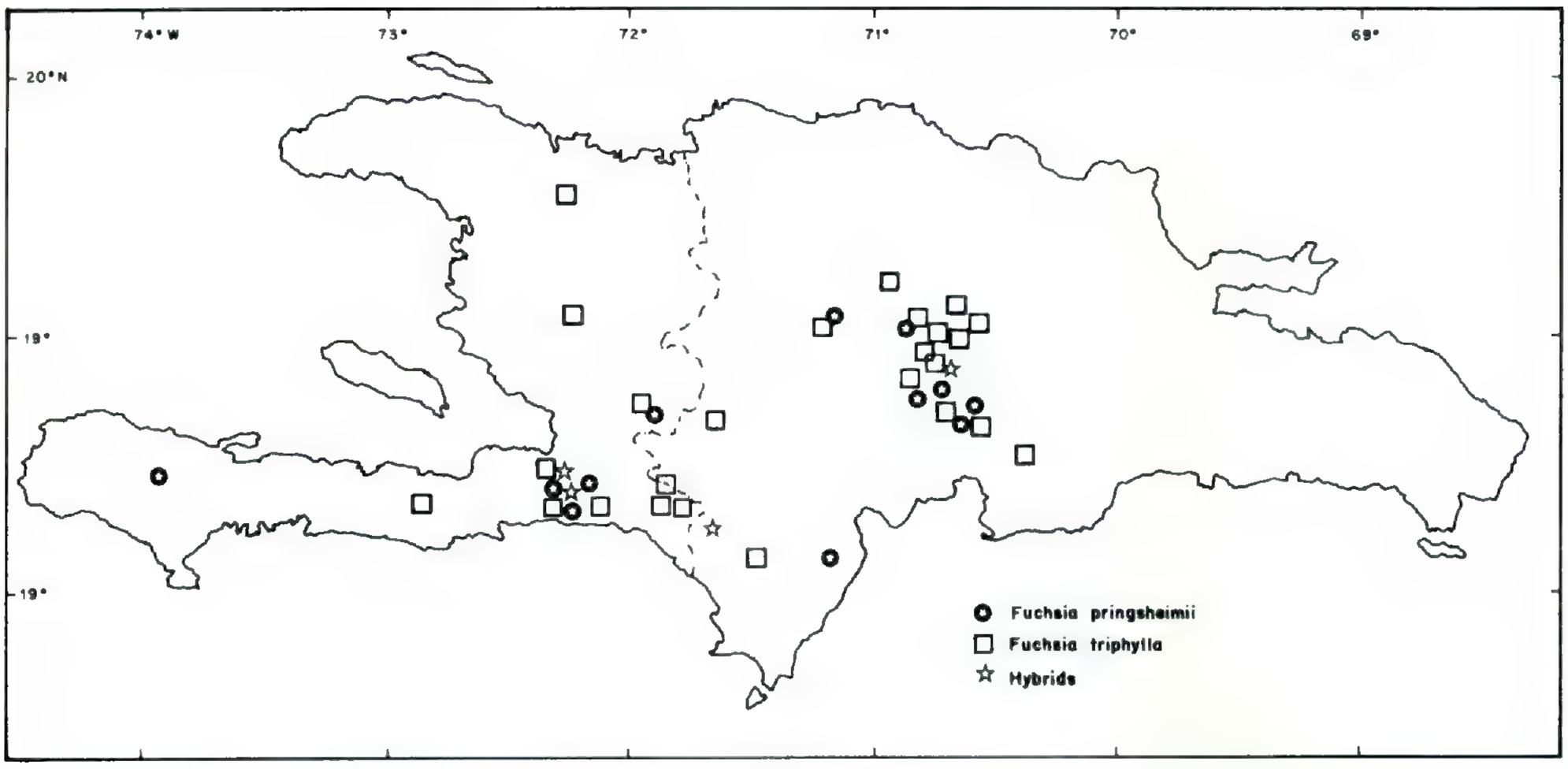


FIGURE 67. Distribution of *Fuchsia triphylla*, *F. pringsheimii*, and naturally occurring hybrids on Hispaniola.

OUT LOCALITY: *Jaeger s.n.* (B, K). DOMINICAN REPUBLIC, AZUA: Loma Nalga de Maco, *Ekman 6304* (S). BAORUCO: without locality, *Howard 12151* (A). LA VEGA: vicinity of Constanza, *Abbott s.n.* (GH, US), *Allard 16446* (US), *Augusto 1150* (A, JBSD), *von Tuerckheim 2956* (BM, F, G, GH, ISC, K, MO, S, U, US, W, Z); between Constanza and Valle Nuevo, *Allard 17422* (US); Jarabacoa, *Augusto 883* (JBSD); Valley Nuevo, *Augusto 1513* (JBSD); El Convento, 10 km S of Constanza to Valle Nuevo, *Berry et al. 3701* (MO, JBSD), *3702* (MO, JBSD); above El Convento, 11 km S of Constanza, *Berry et al. 3703* (MO, JBSD); below La Siberia, new road from Constanza to Valle Nuevo, *Berry et al. 3704* (MO, JBSD); La Siberia, *Berry et al. 3706* (MO, JBSD); S of Jarabacoa, road to Constanza, *Burch & Burch 2546* (CAS, MO); 12 km SE of Constanza, *Davidse 2689* (MO); Loma de Barrero, *Ekman 2057* (G, K); near Jarabacoa, *Fuertes 1619* (A, G, U, W); Río Yaque, *Fuertes 1720* (A, G, W); La Ciénaga, confluence of Río de la Izquierda and Río Los Guanos to form Río Yaque del Norte, *Gastony et al. 149* (GH, US); 8 km S of Constanza, *Gastony et al. 734* (US); Valle Nuevo, *Jiménez s.n.* (DS); Río Grande, Constanza, *Liogier 19453* (JBSD); between Valle Nuevo and Constanza, *Skog 1596* (US); NW of La Ciénaga or La Culata, *Terborgh & Brockman 87* (NA), *88* (NA). PERAVIA: La Nuez, border with Prov. La Vega, *Berry et al. 3712* (MO, JBSD); Sierra de Ocoa, Bejucal, *Ekman H.12039* (A, F, GH, S, US); La Cueva, La Horma Arriba, *Liogier 20999* (JBSD); Plan de Jiguey, *Peña Franjul s.n.* (JBSD). SAN JUAN: Arroyo del Oro, *Canela s.n.* (JBSD), *Howard & Howard 8992* (BM, GH, MICH, S, US). SANTIAGO: Pico de Igua, *Jiménez 1278* (G, US).

This species is easily recognized by its low growth habit, orange flowers, and peculiarly shaped floral tubes. These are nodose at the base, usually strongly constricted in the lower half, then abruptly dilated above the middle, and slightly narrowed again at the rim. *Fuchsia triphylla* can flower when barely woody and just 20–30 cm tall. Its inflorescences are unusual in being nearly erect or nodding in the upper half, although the individual flowers are divergent or drooping as in other species of sect. *Fuchsia*.

Linnaeus based the genus on Plumier's illustration of "Fuchsia triphylla, flore coccineo" (Plumier, 1703). It was a fairly crude drawing showing only four stamens, but the unusual floral tube shape clearly identifies the species, and a more complete habit illustration published later (Plumier, 1757) leaves no doubt that Plumier had illustrated the common Hispaniola fuchsia. Even though Linnaeus stated in the second edition of *Genera Plantarum* (Linnaeus, 1742) that the normal number of stamens in *Fuchsia* is eight, he followed Plumier's plate and placed

the species in the Tetrandria Monogynia in the first edition of *Species Plantarum* (Linnaeus, 1753)..

Philip Miller (1739) reported having *Fuchsia triphylla* in cultivation at his gardens in Chelsea, England. The seeds were sent to him by William Houstoun, presumably before Houstoun's death in 1733, and said to be from "Carthagena, New Spain." Since Cartagena (it is unclear whether he was referring to Cartagena, Colombia or to a Central American locality) is probably a coastal city, it is very unlikely that it was the actual source of Houstoun's seed. He was known to have travelled in Mexico, Cuba, and Jamaica, but not in Hispaniola. A search of Houstoun's and Miller's collections in the Sloane Herbarium at the British Museum failed to find any specimen of *Fuchsia* (J. Lewis, pers. comm.), so we cannot confirm the identification or date of introduction of what otherwise would have been the first introduction of a living fuchsia into Europe.

Lamarck (1788) tried to change the name of *Fuchsia triphylla* to *F. racemosa,* presumably because he found the triphyllous condition very common among the other, recently discovered species of the genus. Lamarck's name was taken up by Descourtilz (1822), who provided an accurate color illustration of the species in his *Flore Médicale des Antilles*. Descourtilz travelled extensively in Haiti from 1799 to 1803 and worked partly in the mines of the Cibao mountains (Massif de la Selle), where he probably found *F. triphylla*. Surprisingly, he mentions having seen this fuchsia several times in "St.-Jago de Cuba," that is, Santiago, a city on the southeastern coast of Cuba. No other reference of herbarium specimen mentions any native fuchsia on Cuba, however, so he may just have seen cultivated plants there. *Fuchsia triphylla* is listed in his work under "plantes stomachiques astrignentes," used as an antipyretic, decongestant, and as a medication in uterine ailments.

Virtually unknown in Europe during the heyday of fuchsia cultivation and hybridization in the early to mid-1800s, *Fuchsia triphylla* was finally introduced into England in 1882, from seeds collected by Thomas Hogg in Hispaniola in 1873 (Hemsley, 1882). It was then cultivated rather extensively and used in interspecific crosses (Wright, 1978b). It is a rather easy species to grow because it is adapted to considerably warmer temperatures than most fuchsias and flowers when only 2–3 dm tall.

In their native range, plants of *Fuchsia triphylla* exhibit considerable morphological variability. Though they generally have a low growth habit, well-developed and woody shrubs with branches several m long have been collected, such as *Berry et al. 3706* (MO), from Prov. La Vega, Dominican Republic. Floral tubes generally maintain their unusual shape described previously, but the degree of constriction and the amount of swelling around the nectary varies substantially within local populations. Leaves are particularly variable in their size, shape, and coloration, and some of this variation is associated with geographically isolated populations on the different parallel mountain ranges that traverse Hispaniola. In the southernmost range, the Sierra de Baoruco in the Dominican Republic and the Massif de la Selle in Haiti, the leaves of most collections are firmly membranous and lanceolate, and they occupy the lower extremes of the species limits in size and number of secondary veins. In contrast, plants from the Cordillera Central in the Dominican Republic vary widely, but are generally much larger, thin-

TABLE 19. Comparison of principal morphological characters of *Fuchsia triphylla* and *F. pringsheimii*.

	F. triphylla	*F. pringsheimii*
Leaf length	2.5–10(–13) cm	1.5–3.5(–4) cm
Petiole length	4–15(–25) mm	1–6 mm
Leaf texture	Membranous	Subcoriaceous
Leaf color	Dull green above, pale to purplish below	Dark glossy green above, white green below
Number of secondary veins	(6–)7–13	3–5
Flower position	Racemose	Axillary
Floral tube length	25–40 mm	19–31 mm
Floral tube shape	Narrowed basally, dilated in the middle, narrowed at the rim	Obconic-funnelform
Flower color	Red orange	Bright red pink
Petal length	6–9 mm	13–24 mm
Petal width	4–6 mm	10–15 mm
Nectary type	Annular, mostly free from the tube	Irregular lobes adnate to the floral tube

ner, and more elliptic than plants from the southern ranges. *Burch & Burch 2546* (CAS, MO) and *Fuertes 1720* (A, G, W) both have leaves reaching 13 cm long and 5.5 cm wide. Plants from this area typically have leaves that are heavily diffused with a purplish coloration, especially on the undersides, but this is by no means ubiquitous in all populations.

Fuchsia pringsheimii is also endemic to Hispaniola. It is morphologically very distinct from *F. triphylla*, as can be seen by a comparison of several morphological characters in Table 19. *Fuchsia triphylla* is much more widespread than *F. pringsheimii*, probably because it is more weedy and occurs at lower elevations. As discussed previously on page 28, the ancestors of these species probably arrived from South America via long distance dispersal. The very marked morphological differences indicate either two separate immigrations or else a wide divergence since the original arrival of a common ancestor. Both species are tetraploid and have biporate pollen, a very unusual combination in the genus, and the two apparently hybridize in nature forming partly fertile hybrids.

A typical altitudinal separation of *Fuchsia triphylla* and *F. pringsheimii* is shown in Figure 5. Although no actual overlap in the altitudinal limits of these species occurs between Constanza and Valle Nuevo, Prov. La Vega, they come very close together around 1,850–1,900 m. A probable hybrid from this approximate altitude was detected, *von Tuerckheim 3541* (BR), in woods below Valle Nuevo, 1,950 m, Aug. 1910. It is intermediate in leaf size, flower position, and flower shape, and has only 30% pollen stainability (400 grains examined). Information on the herbarium label also notes that the plant was growing at an intermediate elevation between populations of *F. triphylla* and *F. pringsheimii*.

A large local population of *Fuchsia pringsheimii* (*Berry et al. 3712*; MO, JBSD) was found interspersed with plants of *F. triphylla* along the edge of a potato field in Dec. 1979 at 2,000 m at La Nuez, on the border of La Vega and

Peravia Provinces in the Dominican Republic. No intermediates or apparent hybrids could be found at that time, but only *F. triphylla* was in flower.

Other hybrids have been detected mostly from Haiti or the Haiti-Dominican Republic border. *Smith & Mejia 10192* (MO, JBSD) is intermediate both florally and vegetatively between the two species; it comes from the Dominican Republic along the Haitian border, Prov. Pedernales, Carretera Internacional between Los Arroyos and Aguacate, in pines at 2,000 m, 10 Nov. 1979. Some of its leaves are 5 cm long with 6 secondary veins (tending toward *F. triphylla*), while the flowers are narrowed in the lower half, yet flare outward at the rim as in *F. pringsheimii*. The petals vary in size from 10 to 16 mm long and 7 to 9 mm wide, intermediate between the two species (see Table 19). The nectary is annular as in *F. triphylla*, and the pollen has numerous aborted, single-porate grains among the plumper bi- and triporate grains. The pollen stainability is 18.7% (500 grains examined). It is interesting that some triporate grains appear here, since both parents have biporate grains. *Jiménez B-4697* (US), from Loma del Toro, in the same province and at the same elevation as *Smith & Mejia 10192*, also shows intermediate morphological characters and has a pollen stainability of under 10%. A final probable hybrid from the Dominican Republic, *Gastony et al. 536* (US), occurs along the Haitian border, but farther north in the Sierra de Neiba at 1,700–2,000 m. It has a pollen stainability of ca. 75%.

In Haiti, *Ekman H.1893* (LL, S) has flowers intermediate between the axillary ones of *Fuchsia pringsheimii* and the racemose ones of *F. triphylla*. It was collected in the Massif de la Selle, Morne Franchant, on the ridge towards Godet, at ca. 1,900 m, Sept. 13, 1920. Except for a slight narrowing toward the rim, its flowers are typical of *F. pringsheimii*, as are the nectaries. The sepals are too short (13–15 mm long) and the petals too small (10–12 mm long and 7–9 mm wide) for that species, however. The leaves of this collection also exceed the normal length for *F. pringsheimii* and have 7 secondary veins. Its pollen stainability is 46.8% (500 grains examined).

Ekman H.1620 (LL, MO, 2 sheets at S, US) is a set of collections in which some specimens appear to be hybrids. The two sheets at S and the one at MO are labelled, "Haiti, Massif de la Selle, Morne Cabaio, near Jardins Bois Pin, ca. 2,000 m, Aug., 1924," but the LL and US sheets say "Marigot" in place of "Morne Cabaio," so it is not clear if they were all collected together. The specimen at S with a typewritten label has numerous, axillary flowers, but constricted floral tubes as in *F. triphylla*. The nectary is an intermediate type between the ring of *F. triphylla* and the adnate nectary of *F. pringsheimii*, and the petals are obovate, but too small for *F. pringsheimii*. Its pollen stainability is 50.4% (500 grains examined). The second sheet at S, with a handwritten label, has flowers shaped much closer to *F. pringsheimii*, with nectaries characteristic of that species. Although its leaves reach dimensions typical of *F. triphylla* (5 cm long, with 7 secondary veins), its pollen stainability is over 90%. The LL sheet has flowers like *F. triphylla* but totally aborted pollen. The MO and US sheets present other combinations of intermediate traits. The wide differences between the different sheets of *Ekman H.1620* may be the result of the segregation of individuals from a hybrid population.

As discussed on p. 31, a single species of hummingbird, *Chlorostilbon swainsonii*, is probably the common pollinator of both *F. triphylla* and *F. prings-*

heimii, and this may help explain the relatively large number of hybrid individuals detected. In addition, severe habitat disturbances have occurred in Hispaniola since the Spanish colonization so that much of the forest vegetation of the island has been eliminated, especially in Haiti (Liogier, 1978). This may have allowed previously separated populations of the two species to enter into closer contact, increasing the chances of intervisitation by *Chlorostilbon*.

60. Fuchsia pringsheimii Urban, Symb. Ant. 1:375. 1899. Barker & Dardeau, Flore d'Haiti 270. 1930. Munz, Proc. Calif. Acad. Sci. IV. 25:33, *pl. 4, fig. 19*. 1943. TYPE: Dominican Republic, Prov. La Vega, near Valle Nuevo, in pines among ferns, 2,100 m, 29 May 1887, *Baron Henrik F.A. Eggers 2159* (B, holotype, destroyed in World War II; BM, G, K, isotypes; photograph of K isotype, MO). Fig. 30.

Erect to scandent shrubs 0.5–2 m tall with ascending to spreading branches. Branchlets terete, puberulent, pruinose, or rarely pilose, reddish purple; older stems with red brown, exfoliating bark. Leaves opposite or ternate, subcoriaceous, narrowly (ob-)lanceolate to elliptic, acute to narrowly cuneate at the base, acute at the apex, 15–35(–40) mm long, 6–15 mm wide, dark rich green and glossy above, subglossy whitish-green to purplish below with red purple veins; upper surface glabrous to loosely strigose, strigose below, especially along the midvein and margin; secondary veins 3–5 on either side of the midvein; margin subentire to glandular-denticulate or dentate, sometimes only toothed in the upper half. Petioles sparsely strigose, 1–6 mm long, red purple. Stipules lanceolate, dark, 1–1.5 mm long, deciduous. Flowers pendant and axillary near the branch tips. Pedicels slender, subglabrous to loosely strigose, 14–40 mm long. Ovary ellipsoid, 6–9 mm long, 2–3.5 mm thick, subglabrous, green to reddish. Floral tube obconic-funnelform, 19–31 mm long, 3–4 mm wide and slightly bulbous at the base, then widened continuously until 9–16 mm wide at the rim, subglabrous outside, glabrous within. Sepals lanceolate, acute to acuminate at the apex, 18–25 mm long, 6–8 mm wide, suberect to spreading at anthesis. Tube and sepals bright red to pink red. Petals red to pink red, broadly obovate, emarginate to broadly truncate at the apex, 13–24 mm long, 10–15 mm wide, slightly spreading and convolute at the base at anthesis. Nectary a yellow-green band lining the basal 2–3 mm of the floral tube, irregularly-lobed and protruding slightly inwards from the tube. Filaments red, 15–18 mm and 12–13 mm long; anthers oblong, 2.5–3 mm long, 1.5–2 mm wide, white to yellow cream. Style red, glabrous; stigma clavate, 4-lobed at the apex, 3–3.5 mm long, 2–3 mm wide, pink to red. Berry oblong, ca. 15 mm long, ca. 8 mm thick; seeds ca. 2 mm thick, ca. 1 mm wide. Gametic chromosome number $n = 22$.

Distribution: Endemic to the island of Hispaniola (West Indies). In Haiti, in the southern Massif de la Hotte and Massif de la Selle ranges and in the central Chaîne des Matheaux, 1,400–2,500 m. In the Dominican Republic, in the southern Sierra de Baoruco, probably in the Sierra de Neiba, and in the Cordillera Central, (1,300–)1,500–2,600 m; low shrubs mostly in pine forests (Fig. 67).

Specimens examined: HAITI, OUEST: Massif de la Selle, Morne La Visite, along path to Saltrou, *Ekman 1450* (US), *1450a* (S), *1450b* (F, G, GH, S); Massif de la Selle, Morne Cabaio road, *Ekman 1613* (S); Massif des Matheaux, Grand-Bois, Morne Moitié-Duportée, *Ekman 5737* (S); Trou Bon

Dieu, Morne La Selle, *Holdridge 1055* (MICH, US). SUD: Morne de la Hotte to mont. Ma Blanche, *Ekman 604* (S). DOMINICAN REPUBLIC, AZUA: Culo de Maco, *Fuertes 1971* (A). BARAHONA: Caña Brava, Monteada Nueva, *Liogier & Liogier 25126* (JBSD). LA VEGA: Valle Nuevo, *Augusto 1495* (A, JBSD), *1507* (A, JBSD), *Berry et al. 3707* (MO), *3709* (MO, JBSD), *3710* (MO, JBSD), *Bueno (Jiménez Herb. #1792)* (A, US), *Jiménez & Withgow 1382* (US); 16 km S of Valle Nuevo, between La Pirámide and La Nevera, *Berry et al. 3711* (MO, JBSD); Valle Nuevo, Loma Atravesada, *Ekman 13851* (S); trail from Los Tablones (2 km W of La Ciénaga) to La Lagunita, *Gastony et al. 287* (GH); 13 km from Valle Nuevo on road to San José de Ocoa, near the pyramid, *Gastony et al. 716* (GH); Alto de Bandera, *Liogier 25224* (JBSD); near Constanza, *von Tuerckheim 3151* (BM, BR, F, G, GH, K, MO, S, U, US, W, Z). PERAVIA: La Nuez, border with Prov. La Vega, *Berry et al. 3713* (MO); San José de Ocoa, Cuchilla del Pino Atravesado, *Ekman 11710* (K, S); La Cueva, La Horma Arriba, *Liogier 20956* (JBSD). SAN JUAN: Sabana Nueva, Piedra del Aguacate to Río del Oro, *Howard & Howard 9014* (B, BM, GH, LE, S, US).

Fuchsia pringsheimii is characterized by its axillary flowers with wide floral tubes and very large, retuse petals, and by its small, dark green, few-veined leaves. It can be distinguished from *F. triphylla,* the other endemic species on Hispaniola, by the morphological features outlined in Table 19. Both species are tetraploid and apparently hybridize in several different localities, even though *F. pringsheimii* is rather infrequent and occurs at higher elevations than *F. triphylla*. The putative hybrids and their pollinator and ecological relationships are further discussed under *F. triphylla*.

Following Munz (1943), *Fuchsia pringsheimii* is included in sect. *Fuchsia,* but with considerable reservation. Its affinities with this section are doubtful because it has a unique combination of features not found in the main body of sect. *Fuchsia* or in any other groups in the genus. These include the large, convolute, and retuse petals, the sepals nearly as long as the floral tubes, the particular non-annular nectary, the reduced leaves, and tetraploidy with biporate pollen. These characters suggest that *F. pringsheimii* may represent an early offshoot of sect. *Fuchsia* that arrived at Hispaniola via long-distance dispersal from South America, or possibly even an earlier line, that was related to the branch of the genus that may have reached Central America before the close of the Paleogene. The other species of *Fuchsia* on Hispaniola, *F. triphylla,* is also tetraploid with biporate pollen, and the two species hybridize in nature, but *F. triphylla* is morphologically much more similar to the Andean members of sect. *Fuchsia* than is *F. pringsheimii*. Therefore, it is possible that two separate colonizations of the genus occurred in Hispaniola.

Some notable variation in leaf size and pubescence occurs between populations from the Cordillera Central of the Dominican Republic and the southern Sierra de Baoruco and Massif de la Selle. Plants from the Cordillera Central have leaves mostly less than 25 mm long and less than 10 mm wide, with rather short, sparse pubescence. In the southern range, most plants have larger and broader leaves 25–40 mm long and 10–15 mm wide. *Ekman 1613* (S), from Haiti, is heavily hirsute-pilose on both stems and leaves. On the Dominican side of the border in Prov. Barahona, *F. pringsheimii* reaches its lowest altitudinal limit at 1,300 m, according to the label of *Liogier & Liogier 25126*.

61. Fuchsia verrucosa Hartweg ex Bentham, Pl. Hartw. 178. 1845. Munz, Proc. Calif. Acad. Sci. IV. 25:58, *pl. 8, fig. 47.* 1943. Rodríguez, Pittiera 6:10, *fig. 1, a–e.* 1974. TYPE: Colombia, Dept. Cundinamarca, on the road between the

Páramo de San Fortunato and the village of Fusagasugá, 1843, *Theodor Hartweg 991* (K Bentham Herb., holotype; BM, BREM, CGE, K Hooker Herb., LE, OXF, P, W, isotypes; photograph of B isotype, POM). Figs. 28, 35, 46, 47.

Fuchsia perbrevis I. M. Johnston, Contr. Gray Herb. 75:30. 1925. TYPE: Colombia, Dept. Cundinamarca, above Sibaté, 3 Jan. 1854, *Isaac F. Holton 892* (NY, holotype; K, isotype).

Fuchsia verrucosa var. *tamaensis* Steyermark, Fieldiana, Bot. 28:440. 1952. TYPE: Venezuela, Edo. Táchira, base of Páramo de Tamá, between Betania and Tamá, near the Colombian border, 2,430 m, 13 July 1944, *Julian A. Steyermark 57175* (F, holotype; NY, US, isotypes).

Erect to scandent, mostly glabrous subshrubs 0.5–2 m tall. Branchlets subterete, 2–4 mm thick, verrucose, green to dull purple; older stems terete, with light gray tan, finely fissured bark. Leaves opposite, firmly membranous, broadly elliptic to obovate, acute to attenuate at the base, acute to acuminate at the apex, 5–16 cm long, 2–8 cm wide, dark matte green above, pale or flushed purple below, often with strigose hairs along the veins; midvein prominent below, secondary veins 10–20 on either side of the midvein, subparallel and anastomosing 1–3 mm before the margin to form a distinct submarginal vein; margin glandular-serrulate. Petioles stout, 5–22 mm long. Stipules firm to semisucculent, (narrowly) triangular, 2–4 mm long, 1–2 mm wide, separate or connate, subpersistent. Flowers solitary in upper leaf axils. Pedicels firm, spreading to drooping, 10–40 mm long. Ovary oblong-cylindric, tetragonous, 10–12 mm long, 2.5–3 mm wide, lustrous light green. Floral tube obconic, 3–6 mm long, 2.5–3 mm wide at the base, 4–4.5 mm wide at the rim, subglabrous inside and outside. Sepals lance-oblong, acute at the apex, 7–11 mm long, 2–4.5 mm wide at the base, spreading to recurved at anthesis. Tube and sepals bright orange or scarlet. Petals red orange, oblong-obovate, 8–9 mm long, 5–6 mm wide, obtuse to subacute at the apex, margin ± undulate, central nerve ± thickened, spreading and convolute at anthesis. Nectary green and composed of 4 distinct antesepalous, ridged lobes ca. 1.5 mm high, ca. 0.5 mm thick, adnate to the base of the floral tube. Filaments light red, 2–3 mm and 1–1.5 mm long; anthers broadly reniform, 1.5–2.5 mm long, 1.5–2 mm wide, white. Style glabrous, stout, red, 6–8 mm long; stigma clavate, slightly 4-cleft at the apex, 2.5–4 mm long, ca. 2 mm wide, light pink to cream, barely exserted beyond the anthers. Berry tetragonous until maturity, ellipsoid or broadly cylindric when ripe, 20–25 mm long, ca. 10 mm thick; seeds 1.4–1.6 mm long, ca. 0.7 mm wide. Gametic chromosome number $n = 22$.

Distribution: Venezuela and Colombia. In the Cordillera Oriental of the Northern Andes from southern Mérida, Venezuela to Huila, Colombia and then on the eastern edge of the Nudo de Pasto in Putumayo; infrequent shrubs in wet, shady banks and along streams; 1,800–3,050 m (Fig. 65).

Representative specimens examined: VENEZUELA, MÉRIDA: road to Mesa de Bustamante, 5 km S of La Playita, between Bailadores and Páramo La Negra, *Tillett & Hönig 738-397* (MO). TÁCHIRA: 6 km E of Zumbador on road to Queniquea, *Berry 3417* (MO); 13 km E of El Portachuelo on road from Bailadores to Pregonero, *Berry 3287* (MO, VEN); 7 km E of El Portachuelo, road to Pregonero, *Berry 3281* (MO), *3662* (MO); El Hato, road to Pregonero, *López-Palacios 1969* (MERF, MO); headwaters of Río Quinimarí, Las Copas, 15 km S of San Vicente de la Revancha, *Steyermark et al. 100577* (MO, VEN); Quebrada Agua Azul, S of El Reposo, *Steyermark & Liesner 118460* (MO, VEN). COLOMBIA, CAQUETÁ: 57 km from Florencia to Altamira, *Luteyn et al. 4954* (COL, MO, NY, US); E of summit between Garzón and Florencia, *Mason 13953* (COL, F, GH, UC, US). CUNDINAMARCA: Barroblanco,

André 1336 (K, NY); Km 34–35 of Bogotá-Sibaté-Fusagasugá road, *Berry 3545* (COL, MO); between Pacho and Río Negro, *García-Barriga 10753* (COL, US); Toquiza, Gazaunta valley, 15 km NW of Medina, *Grant 10260* (COL, NA, RSA); Fusagasugá, *Linden 811* (BM, BR, F, G, K, LE, OXF, W), *Triana 3816* (G, K, P). HUILA: Km 31 of road S of Pitalito towards Mocoa, *Berry 3595* (COL, MO); Gabinete, border with Caquetá, *Cuatrecasas 8465* (CM, COL, F, RSA, US); headwaters of Río Fortalecillas, below Paso de Las Cruces, 39 km E of Neiva, *Fosberg 19787* (RSA, US). META: Páramo de Sumapaz, S of Cordillera de Las Cruces, *Fosberg 20868* (US). NORTE DE SANTANDER: divide between Río La Teja and Río Mesme, between Pamplona and Toledo, *Killip & Smith 19831* (A, F, GH, NY, US), *19976* (A, GH, NY, US); prov. of Ocaña, *Schlim 705* (G, K, P). PUTUMAYO: road from San Francisco to Mocoa, *Mora 4374* (COL); Km 92 from Pasto to Mocoa, *Plowman & Davis 4327* (COL, PSO). SANTANDER: mountains above Bucaramanga, *Barkley & Araque 18S097* (COL, US, VALLE).

This is probably the only species in the genus in which the ovary is clearly longer than the floral tube, and both are quadrangular in transection. It is further characterized by the strictly opposite leaves, verrucose stems, and axillary position of the orange flowers. Vegetatively and geographically, *Fuchsia verrucosa* is consistent with its placement in sect. *Fuchsia,* but its extremely short floral tubes, antesepalous nectary lobes, smooth viscin threads, and tetraploidy with biporate pollen are anomalous in this section. The nectary and small flower size of *F. verrucosa* are most like those of the Central American *F. jimenezii* (sect. *Jimenezia*), but that species has smaller, terete ovaries, paniculate inflorescences, and a reflexed whorl of stamens. *Fuchsia verrucosa* occurs sympatrically with seven other species of sect. *Fuchsia* (*F. cuatrecasasii, F. gehrigeri, F. hirtella, F. nigricans, F. scabriuscula, F. sessilifolia,* and *F. venusta*), and despite searches in the field and in herbarium specimens, no apparent hybrid plants were found, further indicating a lack of close relatives in sect. *Fuchsia*. Experimental crosses with species such as *F. jimenezii, F. pringsheimii,* and other species of sect. *Fuchsia* might help elucidate the affinities of this species.

UNCERTAIN SPECIES

Fuchsia miniata Planchon & Linden, Fl. Serres Jard. Eur. 8:7, *pl.* 1852. LECTOTYPE: the illustration in the preceding citation, cultivated in Belgium (?) in 1852 by Jean-Jules Linden, from seeds collected in Colombia by M. Schlim.

The illustration and short description provide insufficient detail to characterize this species adequately. Although the illustration closely resembles *F. crassistipula,* the conspicuous stipules of that species are not present in the plate, and the description specifically mentions the stems as terete, whereas in *F. crassistipula* they are conspicuously ridged. A copy of the published illustration is in the herbarium at Montpellier, France (MPU), where Planchon did much of his work. The plate is accompanied in the same folder by several fragments of what appears to be *F. gehrigeri,* but these fragments are not attached to the herbarium sheet and do not seem to correspond to the illustration.

Fuchsia platypetala I. M. Johnston, J. Arnold Arbor. 20:241. 1939. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):561. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:30, *pl. 3, fig. 16.* 1943. TYPE: Peru, Dept. Apurimac, Chincheros, along lanes in town, semi-cultivated but reported wild nearby, 2,930 m, 1 Nov. 1935,

James West 3705 (UC, holotype, not seen; GH, MO, isotypes; photograph of GH isotype, NY).

This entity is known only from cultivated material from Depts. Apurimac and Cuzco of southern Peru, and no collections more recent than 1946 have been seen. The plants are axillary-flowered with large, obovate petals that are somewhat mottled when dry. They also have reflexed sepals, which strongly suggests a relationship to *Fuchsia boliviana,* a species extensively cultivated nearby, but with long, racemose inflorescences. Other plants referrable to *F. platypetala* are *Vargas 6267* (CUZ), from the town of Pumamarca, Dept. Cuzco, 3,400 m, and *Herrera 1514* (GH), from the city of Cuzco. Most likely these represent hybrids of *F. boliviana* with some other axillary flowered species of the region such as *F. denticulata* or *F. austromontana,* both of which have petals that dry streaked or mottled as in the specimens cited above. Whereas the pollen stainability of the type collection is high, the pollen of *Herrera 1514* is totally aborted.

Excluded Species

Fuchsia involucrata Sw., Prodr. 62. 1788. = *Urceolaria involucrata* (Sw.) Standl., N. Am. Flora 32(2):132. 1921. (Rubiaceae).

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POLLINATOR MAINTENANCE VS. FRUIT PRODUCTION: PARTITIONED REPRODUCTIVE EFFORT IN SUBDIOECIOUS *FUCHSIA LYCIOIDES*

PETER R. ATSATT AND PHILIP W. RUNDEL[1]

ABSTRACT

Populations of *Fuchsia lycioides* Andrews are composed of small-flowered female plants and an equal number of larger-flowered hermaphrodites, which may be female fertile, or morphologically or physiologically female sterile. A major selective force driving the evolution of separate sexes in *F. lycioides* is suggested to be the partitioning of limited resources associated with pollinator maintenance and fruit production in a semi-arid mediterranean climate. The hummingbird *Rhodopsis vesper atacamensis* is the only known pollinator, and appears to be energetically dependent upon *F. lycioides*. Hermaphrodites are facultative in their fruit production, produce as much as six times more nectar than females, and feed birds both prior to flower opening and during anthesis. Females bear abundant fruit and produce only a relatively small amount of nectar during anthesis. Nectar production is extremely variable in both sexes but is unpredictable in hermaphrodites and apparently predictable in females. The unpredictability of hermaphrodite nectar production may be a key factor permitting the evolution of resource partitioning into large-flowered bird-feeding pollen plants and small-flowered reproductive individuals.

Subdioecy, a state of dioecy in which populations regularly contain imperfectly differentiated individuals in addition to strictly unisexual individuals, has evolved by at least five evolutionary pathways (Ross, 1982). The genus *Fuchsia* is characterized by the hermaphroditism–gynodioecy–subdioecy pathway, wherein the male sterile mutants among the hermaphrodites produce the gynodioecious state, followed by a gradual reduction of seed fertility of hermaphrodites so that these come to function largely or completely as males (Godley, 1955; Breedlove, 1969; Arroyo & Raven, 1975).

The selective forces apparently responsible for the evolution of dioecy have recently been reviewed by Ross (1982), who emphasized that many of the proposed selection models (fertility variation, sexual selection, overdominance, and resource allocation) are scarcely or not at all distinct from each other. Cases involving pollinator influence, fruit dispersal, and predation (Bawa, 1980; Givnish, 1980) are also likely to involve differential resource allocation. If so, perhaps the most generalized model for the evolution of dioecy is simply an energetic argument: that female reproductive effort is largely limited by the availability of physiological resources, and that separation of the sexes increases fitness by allowing more efficient use or allocation of limiting factors. The resource allocation model need not exclude the traditionally considered hypothesis of outbreeding advantage (inbreeding depression). Ross (1982) concludes that outbreeding advantage is not always a factor in the evolution of dioecy, and even where it occurs, it is probably accompanied by other selective forces. Freeman et al. (1980a), and Bawa (1980) have expressed similar views.

In this paper we report observations on the floral biology of a facultatively

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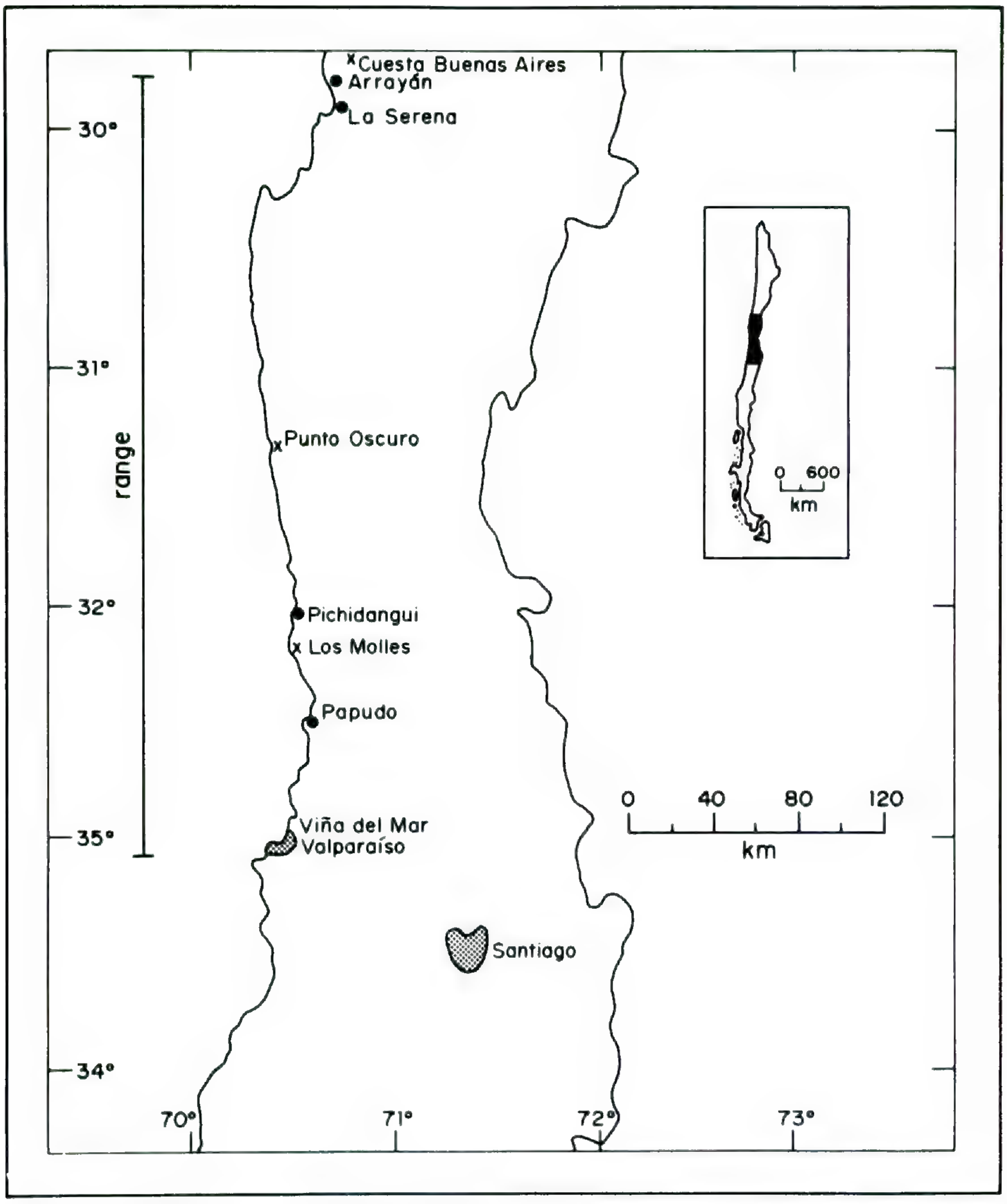

FIGURE 1. The geographic range of *Fuchsia lycioides* and the location of study sites along the coast of central Chile.

subdioecious shrub, *Fuchsia lycioides* Andrews, and examine evidence consistent with the hypothesis that differential resource allocation (related to pollinator maintenance) may be an important selective force favoring the evolution of separate sexes in this species.

Fuchsia lycioides, forming the monotypic section *Kirschlegeria* of the genus, is restricted to a narrow coastal belt in the Mediterranean-climate zone of central Chile (Fig. 1) in a relatively severe environmental regime with only moderate winter precipitation and long dry summer conditions. At its southern limit south of Valparaiso, mean annual precipitation is 460 mm/yr while at its northern limit north of La Serena there is only slightly more than 150 mm/yr. Mean growing season temperatures vary little over this latitudinal range.

Ecologically, *F. lycioides* is characteristic of bluff communities along the immediate coast where it occurs in mixed stands of deciduous and evergreen shrub

species. On typical sites such as those at Pichidangui (Coquimbo Province) it occurs with other woody deciduous shrubs (*Adesmia arborea* and *Proustia pungens*), a mixed assemblage of deciduous semiwoody shrubs, and the evergreen *Lithraea caustica*. On exposed rocky headlands, as at Los Molles (Aconcagua Province) just south of Pichidangui, however, *F. lycioides* occurs in a predominately evergreen community dominated by *Lucuma valparadisea*. Further north at Punto Oscuro, and near La Serena, it occurs in a community strongly dominated by the shrubby *Oxalis gigantea*, a desert floristic element. In all of these varied community types, *F. lycioides* remains an important (dominant) species.

METHODS

Field observations and data were collected over the entire range of the species in Chile, at Papudo, Los Molles, Pichidangui, Punto Oscuro, Arrayan, and Cuesta Buenos Aires, in the years 1974, 1975, 1977, and 1978. Differences between hermaphrodite and female flowers were characterized by measuring flower tube length and style length in one southern (Pichidangui) and one northern (Arrayan) population. Data were also collected on style abortion in hermaphrodites, and the ratio of female to hermaphrodite individuals was determined at four sites.

The standing nectar crop was measured by sampling flowers with 10 lamda micropipets. In the field, buds were sampled in late afternoon by puncturing the base of the closed flower tube with a micropipet. Open, non-pollinated flowers (lacking white pollen on the red stigma) were sampled between 800 and 1000 hours. Nectar was measured for a series of marked flowers in the late afternoon, and the flowers were then bagged and remeasured the following morning to determine overnight nectar production. Nectar productivity was also measured from three plants each of female and hermaphrodite individuals raised from seed in the greenhouse. Flowers were tagged and measured at 1700 hours on the first, second, and third day after opening.

RESULTS

FLORAL BIOLOGY

The rose-colored, dimorphic flowers of *F. lycioides* have four sepals, four small petals, and a cylindric floral tube. The open cup-shaped floral tube of the female flower is usually 1.5–3 mm long, with a 6–10 mm style at our primary study site at Pichidangui. Eight reduced anthers are present but do not contain pollen. The larger hermaphrodite flowers are 2.5–5 mm long, with style length ranging from 14–22 mm. Although tube length of the two flower types may occasionally overlap, there is a sharp gap of 3.5–4 mm between maximum style length in the small female flowers and minimum style length in the larger hermaphrodite flowers (Fig. 2). Flowers of the Arrayan population show the same pattern but are smaller in size, particularly with regard to maximum style length, reflecting the considerably drier conditions under which these plants were growing.

A variable proportion of the flowers on hermaphrodite plants lack styles and are therefore functionally male. The percentage of male flowers on hermaphrodite plants was quantified in the northern Arrayan and Cuesta Buenos Aires popula-

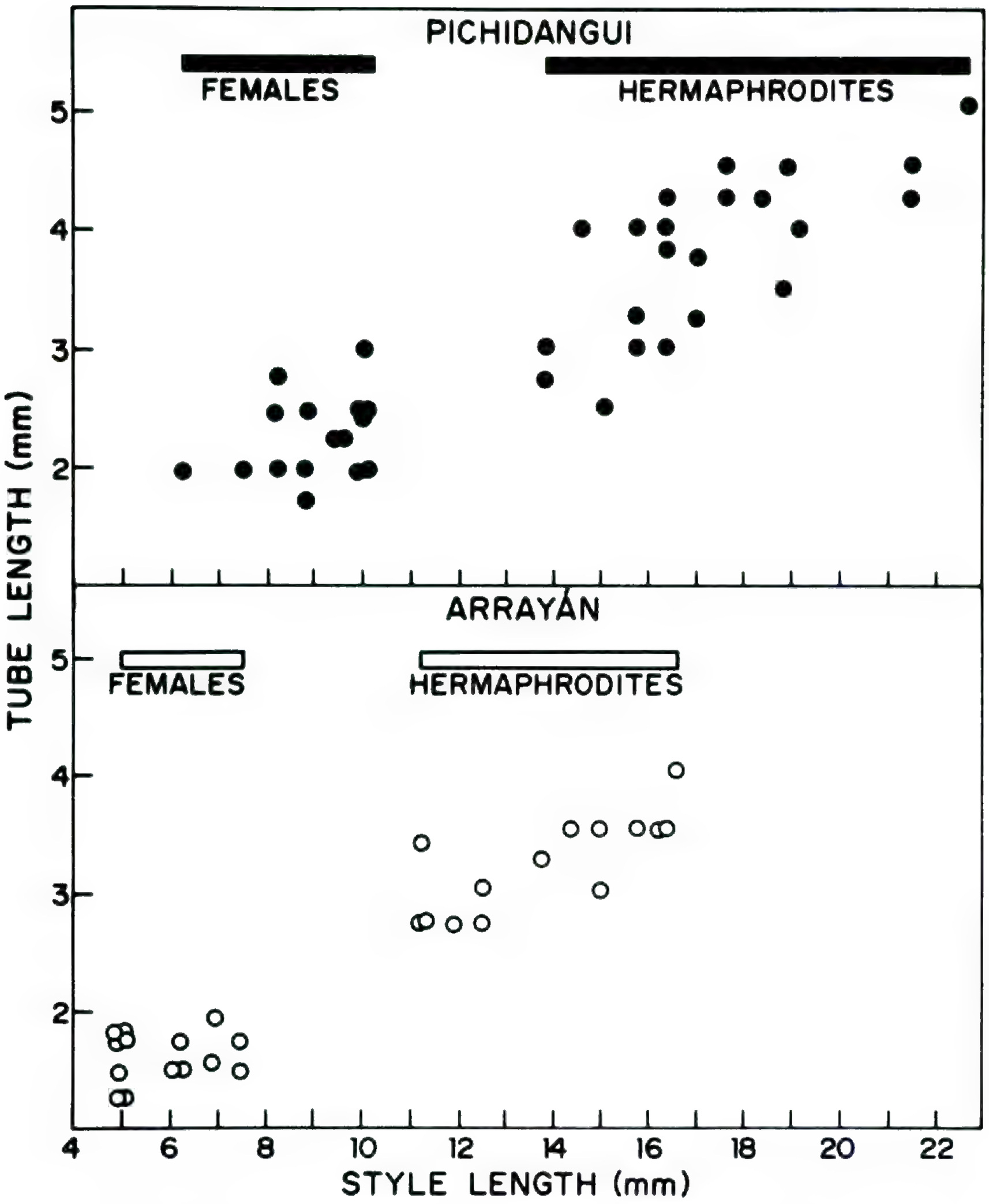

FIGURE 2. Flower size in a northern and southern population of *Fuchsia lycioides*. Note that the style lengths of hermaphrodites and females are variable but well separated.

tions by recording the proportion of aborted styles in ten randomly chosen flowers on each of 28 "hermaphrodite" individuals (Fig. 3). One-quarter of these plants had all perfect flowers. In the remaining individuals the percentage of male flowers ranged from 10 to 100%. Although similar data were not collected at the southern Pichidangui population, the frequency of individuals with high proportions of flowers with aborted styles was observed to be very low. The Pichidangui site is considerably more mesic than the northern population, suggesting that style condition may be influenced by moisture stress.

Perhaps the most striking difference between female and hermaphrodite individuals, other than flower size, was the presence of abundant fruit on female plants and its general absence on hermaphrodites. At Pichidangui, for example, all female plants sampled in 1974 produced fruit, with a mean of 11.4 berries per new shoot. In contrast, 81% of 26 hermaphrodites sampled produced no fruit,

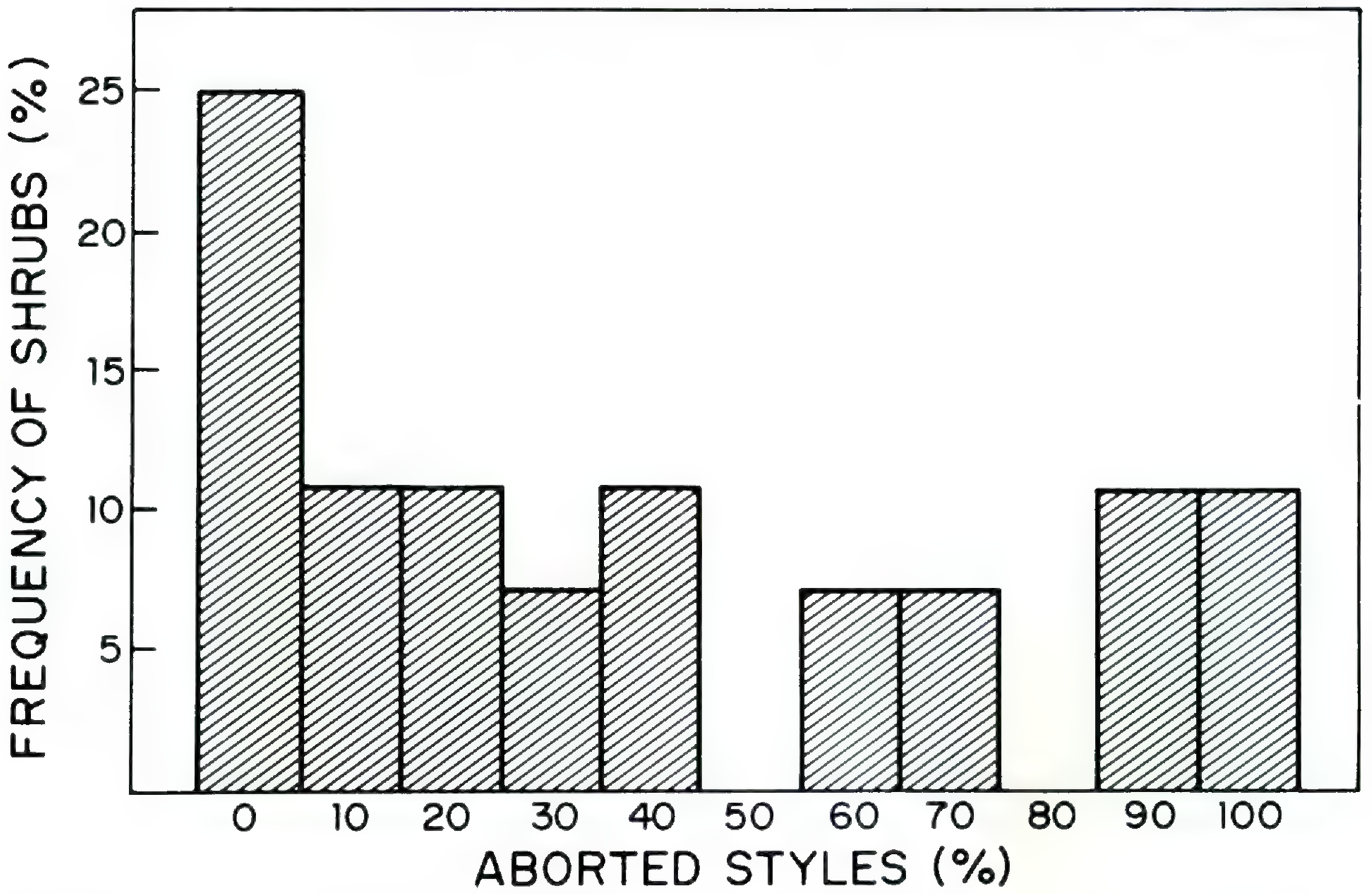

FIGURE 3. The percentage of male flowers (aborted styles) on hermaphrodite plants in the northern Arrayan and Cuesta Buenos Aires populations.

and the remainder bore only a small number per plant. These were positioned in the axils of new shoots, suggesting that they were produced very early in the growing season, before shoot expansion occurred. Similar patterns of fruit production were observed at nearby Los Molles, and the northern Arrayan and Cuesta Buenos Aires sites. However, at Punto Oscuro in the central part of the species range, a single large population was sampled in which a majority of the hermaphrodites bore abundant fruit in 1974. The seeds within the hermaphrodite berries were normal with respect to both quality and quantity, and readily germinated when later planted.

The ratio of hermaphrodite to female individuals is not different from expected frequencies based on a 50:50 sex ratio for all sites (all χ^2s between 0.04 and 0.190). The percentage hermaphrodites and sample sizes were: Pichidangui 51%, n = 100; Papudo 48%, n = 50; Arrayan 53%, n = 41; Cuesta Buenos Aires 53%, n = 53. The sexes showed no apparent differences in microhabitat distribution, although this was not quantified beyond our estimation that similar proportions of each sex occurred in the small homogeneous areas we examined.

POLLINATION

The only known pollinator of *F. lycioides* is a small, extremely timid hummingbird, *Rhodopsis vesper atacamensis* Leybold. This small-billed race (22.9 mm) of the larger northern subspecies (bill length 30.7 mm) is known only from the coastal areas inhabited by *F. lycioides*, and appears to be largely energy dependent upon this species. There is an interesting similarity between bill length in *Rhodopsis vesper atacamensis* and maximum style length of *Fuchsia lycioides*

TABLE 1. Hermaphrodite flower piercing and pollination at three sites.

	(N)	Number of Buds Pierced	Number Pierced Flowers Polli-nated	Total Number Flowers Polli-nated	% Buds Pierced	% Pierced Flowers Polli-nated	% Total Flowers Polli-nated
Pichidangui	(279)	70	64	229	25	91	82
Pichidangui canyons	(21)	13	9	13	62	69	62
Papudo	(76)	69	33	37	91	48	49

(Fig. 2). At Pichidangui, hummingbird activity was observed only prior to 1000 hours, along the margins of the coastal headlands, and again in the late afternoon on the steep canyon slopes facing the sea. During morning activity the birds visit numerous flowers per plant, and move rapidly between hermaphrodite and female individuals with no obvious pattern of foraging or territoriality.

A consistent feature of flowers from all populations was the common presence of a hole at the base of the floral tube, attributable to piercing activity by *Rhodopsis*. Although we did not witness piercing, buds tagged in midafternoon were pierced by 10 am the following day. No insect other than an occasional honeybee was ever observed in or about the flowers. A few honeybees were found gathering pollen from hermaphrodite flowers, but their visits were easily distinguished by the presence of stringy masses of pollen hanging from the style and stigma. Honeybees were never observed at female flowers, which are also occasionally pierced. No evidence of chewing by bees or other insects was found in hundreds of observations. Bud piercing appears to occur chiefly in the evening since the rim of the pierced hole is discolored by the time the flower opens the following day. Piercing activity is predominately but not exclusively associated with the larger hermaphroditic buds.

The frequency of hermaphrodite piercing at three sites and its apparent relationship to pollination efficiency is given in Table 1. On the bluffs at Pichidangui, where a massive number of flowers were available in 1974, only one-quarter of the hermaphrodite flowers were pierced. Nevertheless, nearly all (91%) of these pierced buds received a return visit after opening, as evidenced by the presence of pollen on the stigmas of flowers with discolored holes. In the more protected canyons below these bluffs, 62% of the hermaphrodite flowers were pierced, but only 69% of these received return visits effecting pollination. At Papudo, where nearly all hermaphrodite flowers were pierced, hermaphrodite pollination dropped to 48%. Female flowers were rarely pierced at Pichidangui, but at Papudo, where 91% of all hermaphrodites were pierced, 27% of the small female flowers also had holes at the base of the floral tube. Comparison of the three sites suggests that overall pollination activity (return visits to open flowers) decreases significantly as the frequency of piercing increases. Despite considerable site variation in the frequency of flower piercing (25–91%) and total pollination (82–49%), the frequency of pollination of pierced flowers does not differ significantly from the frequency for unpierced flowers, demonstrating that individuals providing bud nectar are not at a selective disadvantage as pollen donors.

TABLE 2. Standing nectar crop (field) and productivity (greenhouse) of hermaphrodite and female flowers. Data in μl.

		Hermaphrodite			Female		
		n	Mean	Range	n	Mean	Range
Field	Mature buds	18	1.72	0–3.6	12	0.21	0–0.8
	Day 1 flowers	155	1.88	0–7.0	70	0.80	0–2.9
Greenhouse	Day 1	10	3.81	0–6.2	9	1.10	0–1.6
	2	10	1.84	0–3.2	9	0.00	—
	3	10	0.76	0–1.8	9	0.00	—
	Total		6.41			1.10	

NECTAR PRODUCTION

Hermaphrodite flowers produce an average total of six times more nectar than do female flowers under greenhouse conditions (Table 2); they yield approximately 1.8 μl per 24 hour period, beginning 12–36 hr before flower opening, and continuing for two days thereafter. Nectar productivity drops to 0.76 μl on the third day after opening, and flowers usually wilt the next day. Female flowers produce very little nectar in bud, contain approximately 1 μl at the end of the first day after opening, and then usually cease to produce nectar. Maximum yields sometimes reach 2 μl (Fig. 4).

Variation in nectar production is the most striking and consistent feature observed in both field and greenhouse samples (Fig. 4). In the field, we found it impossible to predict nectar availability in hermaphrodite flowers using size, color, developmental state, and stigma condition as indicators (only flowers without pollen on the stigma were sampled). All plants produced nectarless flowers, plus flowers of low, intermediate, and high productivity. The greenhouse sampling demonstrated a similar pattern. Although females also produce nectarless flowers, nectar availability can nevertheless be assessed visually, since the eight large anthers that block the entrance to hermaphrodite flowers are absent. In contrast to the pendulous hermaphrodite flowers, the female flowers are held upright or at right angles to the ground, and the nectar is easily visible when the short floral tube is filled.

DISCUSSION

Fuchsia lycioides represents one of four instances in the genus *Fuchsia* in which male sterility has arisen independently in a small section with a distribution marginal to that of the genus as a whole (Raven, 1979). Floral morphology is misleading in this species and functional sex requires a physiological rather than a morphological definition (Ross, 1982). The female plants retain a set of small sterile anthers, and the hermaphrodite individuals produce two morphological types, perfect flowers, and styleless flowers. Superimposed on this morphological pattern is that fact that perfect flowers can also be female sterile. Both morphological and physiological female sterility may be influenced by environmental stress. Aborted styles were rarely observed at Pichidangui, but the absence of styles was a noticeable feature in the more northern, drier sites. However, even

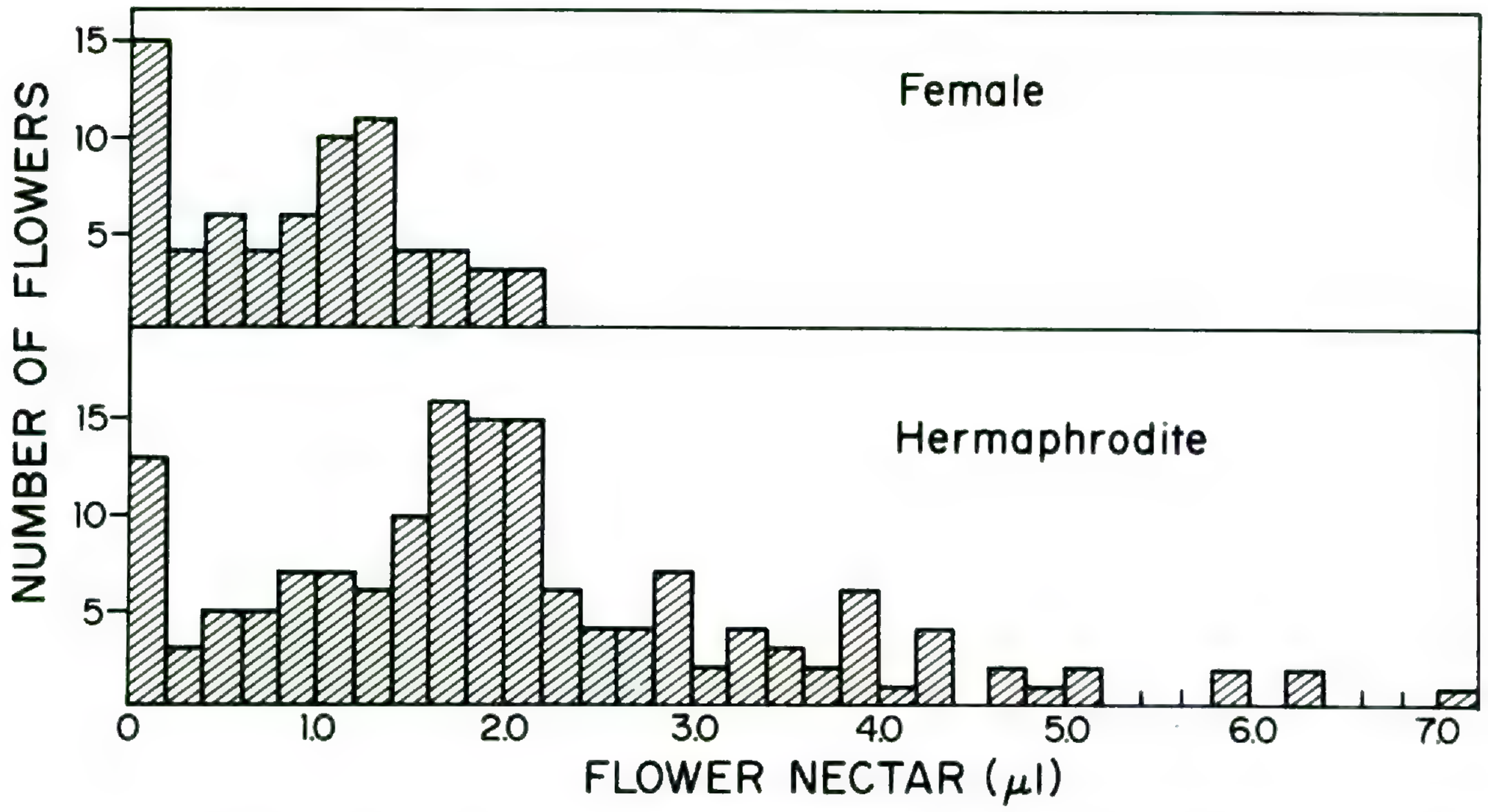

FIGURE 4. The standing nectar crop in open, non-pollinated non-pierced flowers at Pichidangui, a site with high flower density.

individuals with 100% styleless flowers on the date of our sample in 1974 bore a few fruits, demonstrating that the proportion of obligate male flowers changes seasonally. Individuals of many dioecious and subdioecious species are able to alter their sexual state in response to changes in the ambient environment and/or changes in size or age (Freeman et al., 1980b). Temperature is known to affect female fertility in perfect hermaphrodites of other gynodioecious *Fuchsias* (Arroyo & Raven, 1975). Under greenhouse conditions hermaphrodites of *F. thyifolia* and *F. microphylla* that were normally female sterile throughout the spring and summer months produced some fruit by self-pollination when greenhouse temperatures were lower at the onset of winter. A similar mechanism could account for the few scattered fruits found on hermaphrodites in most populations of *F. lycioides* early in the growing season. Examination of herbarium specimens and reports from local residents suggest that at least some individuals of *F. lycioides* may be in flower from August through April, with some evidence existing for distinct peaks in flowering at irregular intervals. This condition may be related to precipitation patterns. Late in the season, particularly from January to April, flowering may be confined to a few individual branches on a shrub, indicating physiological compartmentalization of phenological development. Few other associated species are able to flower under the water stress conditions of this summer period. We do not know if *Rhodopsis* is present throughout the year.

Although we observed what appeared to be indiscriminate visitation to both sexes by *Rhodopsis*, it was not immediately clear why the bird should visit female plants when hermaphrodites were available. However, if *Rhodopsis* is no more efficient than we were when foraging at hermaphrodite flowers, the increased cost of searching time within large-flowered plants may significantly reduce the benefits gained when large nectar strikes occur. Within small-flowered plants, the bird should be able to recognize full floral tubes and therefore consistently forage

at flowers with a time/energy yield equal to or greater than the average productivity of the unpredictable hermaphrodites. A system with inequality of nectar production appears to function only because each hermaphrodite flower must be sampled to detect its variable reward, while this may not be true for open, upright female flowers.

Bud piercing is presumed to be an indicator of energetic stress in *Rhodopsis*, since its frequency varies with resource concentration. At Pichidangui, where shrub and flower densities were very high, flower piercing was relatively low and most flowers were visited legitimately (Table 1). Bud piercing increased in Pichidangui canyons, where individual plants were widely separated, and at Papudo, where flower production was very low. The lower pollination efficiency associated with reduced availability of bud nectar (Table 1) suggests that *Rhodopsis* is forced to decrease its foraging time in populations lacking this energy supplement.

Lloyd & Webb (1977) argued that male reproduction effort is likely to be less than that of females, unless extraordinary quantities of pollen are required either to achieve high fertilization levels or for indirect contributions to fitness such as pollinator rewards. We believe that pollinator maintenance may be a pivotal condition for the persistence of *F. lycioides* in its present arid environment, and thus a major selective force driving this species toward functional dioecy. Bird pollination is rare among dioecious species (Bawa, 1980), perhaps because energetically expensive pollination systems are selected against if nectar production and ovules utilize the same resources and limit each other's production within the female. Under these conditions selection for decreased energy allocation to nectar (by shifting to small insect pollination) might be expected to precede or evolve concurrently with dioecy. Indeed, such a shift appears to have occurred in the gynodioecious and dioecious *Fuchsias* that inhabit temperate and cool-temperate mountain forests in Mexico and Central America. Four species attract both bees and hummingbirds, but bees (primarily *Bombus*) appear to be the more frequent visitors. Three taxa have shifted from having red flowers to having smaller white flowers and are pollinated solely by long-tongued tachinid flies (Table 1 in Breedlove, 1969). This option has apparently been unavailable on the coastal bluffs of central Chile, where potential insect pollinators are scarce. Although relatively calm conditions prevail during the early morning and late afternoon, strong onshore winds occur during most of the day, making it extremely difficult for most pollinators to forage. *Fuchsia lycioides* is apparently forced to maintain a high-energy-requiring pollinator at a cost that directly competes with the energy demands of fruit production in an environment with low and unpredictable winter precipitation and long summer droughts. The solution would appear to be the evolution of resource partitioning into large-flowered bird-maintaining pollen plants and small-flowered reproductive individuals. This hypothesis explains the disproportionately greater daily nectar production of hermaphrodites and the coincident development of female sterility by these individuals.

Male-predominant sex ratios are a pronounced feature of many long-lived dioecious species. Most such skewed ratios are thought to be caused by higher female mortality rates, specifically, differential post-reproductive mortality associated with differences in reproductive effort (Lloyd, 1973; Lloyd & Webb,

1977). The numerical equality of the sexes in *F. lycioides* is consistent with our contention that each makes a functionally separate but energetically similar contribution to reproductive effort. While a resource partitioning hypothesis appears attractive in this case, this argument does not necessarily exclude nor diminish the importance of outcrossing enforcement as one of several factors contributing to the evolution of subdioecy in *F. lycioides*.

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THE MEXICAN AND CENTRAL AMERICAN SPECIES OF *FUCHSIA* (ONAGRACEAE) EXCEPT FOR SECT. *ENCLIANDRA*[1]

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ABSTRACT

Six native and one naturalized species of *Fuchsia* (Onagraceae) from Mexico and Central America are recognized, not including the recently revised sect. *Encliandra*. One species, *Fuchsia jimenezii*, and one section, *Jimenezia*, are newly described, and *Ellobium* is also recognized as a section. The recognition of subdioecy in *Fuchsia paniculata* (sect. *Schufia*) now strengthens evidence of a trend toward male sterility and eventual dioecy in the small, peripheral sections of the genus. The distinctions between that species and the closely related but entirely hermaphroditic *F. arborescens* are established. *Fuchsia jimenezii* (sect. *Jimenezia*) is a phylogenetically key species because it has the antipetalous stamens reflexed into the tube like sect. *Encliandra*, yet it has the more generalized many-seeded berry and hermaphroditic flowers of most other sections. The new sect. *Ellobium* joins *F. splendens*, *F. fulgens*, and *F. decidua* into a morphologically and geographically coherent unit, with links to the Andean sects. *Fuchsia* and *Hemsleyella*. *Fuchsia cordifolia* is reduced to the synonymy of *F. splendens* on the basis of a study of populations from throughout its range.

Fuchsia is a predominantly South American group comprising some 100 species of shrubs and trees. In the only comprehensive revision of the genus, Munz (1943) recognized seven sections, *Quelusia*, *Fuchsia*, *Hemsleyella*, *Kiershlegeria*, *Schufia*, *Encliandra*, and *Skinnera*, of which the last three, a small part of sect. *Fuchsia*, and one species of *Hemsleyella* were found outside of South America. Recently, Breedlove (1969) revised the Mexican and Central American sect. *Encliandra*, reducing the number of species recognized from 16 to 6 through the study of populations in the field. Later, experimental work by Arroyo & Raven (1975) revealed that the three morphologically gynodioecious species in this section are functionally subdioecious and that the remaining morphologically dioecious species probably evolved from gynodioecious ancestors via subdioecy. As a result of the senior author's extensive field experience in the area, the examination of numerous specimens, and especially the finding in Central America of sexually dimorphic populations in sect. *Schufia*, there was good reason to revise critically the remaining species of the genus in Mexico and Central America.

Outside of sect. *Encliandra*, we here recognize six species of *Fuchsia* in three sections, all of which are endemic to Mexico and Central America. Two of these sections, *Ellobium* and *Jimenezia*, are newly recognized in this paper. Section *Ellobium* comprises three species, *F. splendens* (including *F. cordifolia*), *F. fulgens*, and *F. decidua*. The first two species were placed by Munz in the large

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0026-6493/82/0209–0234/$02.65/0

sect. *Fuchsia,* while *F. decidua* was placed with other tuberous shrubs and epiphytes in sect. *Hemsleyella.* With the present change, *Hemsleyella* now consists entirely of apetalous species that are confined to the South American Andes. Likewise, sect. *Fuchsia* is now restricted in its native range to the Andes except for two species that are endemic on the island of Hispaniola.

Fuchsia jimenezii, the only member of sect. *Jimenezia,* is newly described from Panama and Costa Rica. It is the only member in the genus outside of sect. *Encliandra* that has the antipetalous stamens reflexed and included in the floral tube. It differs strongly from *Encliandra,* however, in its hermaphroditic flowers in a terminal inflorescence and in its more generalized many-seeded fruits. The stamen character is clearly apomorphic and indicates that sect. *Jimenezia* is the sister group of the generally more specialized sect. *Encliandra.*

The presence and distribution of male sterility was not fully recognized in sect. *Schufia* until now. *Fuchsia arborescens* is entirely hermaphroditic and is confined to the area north of the Isthmus of Tehuantepec. In contrast, the Mexican and Central American *F. paniculata* has hermaphroditic populations north of the Isthmus and morphologically gynodioecious but functionally subdioecious populations from Chiapas, Mexico, to Panama. The discovery of subdioecy in sect. *Schufia* is significant in view of the fact that three other geographically peripheral sections of *Fuchsia,* namely *Encliandra* (six species; Mexico and Central America), *Skinnera* (four species; New Zealand and Tahiti), and *Kierschlegeria* (one species; dry, coastal Chile), are characterized by male sterility in all but one species of sect. *Skinnera* (Arroyo & Raven, 1975). All of the New World species and one species in New Zealand are dioecious or subdioecious; the remaining two New Zealand species are gynodioecious. These constitute the only known cases of male sterility in Onagraceae (Raven, 1979). *Fuchsia paniculata* is noteworthy in being the only species in the genus to include both hermaphroditic and sexually dimorphic populations. Since hermaphroditic individuals of *F. paniculata* give rise to both pistillate and perfect-flowered individuals, the genetic control of male sterility in sect. *Schufia* is unlike that of sect. *Encliandra,* where it is apparently controlled by a dominant gene (Arroyo & Raven, 1975). It may be more similar to the kind of male sterility found in the distantly related sect. *Skinnera,* where it is controlled by a recessive gene (E. Godley & P. Raven, pers. comm.).

In addition to the native species, one commonly cultivated and naturalized species native to South America, *Fuchsia boliviana,* is included in this treatment. Since its relationships lie mainly outside of the area considered in this paper, its complete synonymy is not presented here (see Berry, this number, pp. 162–163).

HISTORY OF CULTIVATION

All the Mexican and Central American species treated here, except *Fuchsia decidua* and *F. jimenezii,* were brought into cultivation in the past century. George Bullock first introduced *F. arborescens* into Europe in 1823 from seeds he obtained in the botanical garden in Mexico City (Bullock, 1824). It is quite likely that these same plants were originally collected by Martín Sessé, an early collector of the Mexican flora and founder of the botanical garden in 1787 (McVaugh,

1977); Sessé's own name for this species, *Fuchsia arborea,* was validly published only in 1888.

Fuchsia fulgens arrived in Europe in the 1830s, probably first introduced by Theodor Hartweg from Mexico in 1836. *Fuchsia splendens* reached Europe in 1840 from Guatemala under the name *F. cordifolia,* again through the remarkable collecting efforts of Hartweg, who sent more seeds of this species the following year from southern Mexico. Both of these species were purportedly involved in many of the early hybridizations with strains of *F. magellanica* Lam. from South America (see Harrison, 1841; Hemsley, 1876), possibly playing a role in the origin of the commonly cultivated garden hybrids now grouped under the name *F. hybrida* Hort.

The first record of *F. paniculata* in cultivation was in 1847 by the Van Houtte nurseries in France, from seeds sent from Guatemala. This species is now widely cultivated in parks and botanical gardens throughout the world, whereas its close relative *F. arborescens* is not found frequently in cultivation today. *Fuchsia paniculata* has apparently become naturalized in Sri Lanka, Tanzania, and Hawaii. In addition, Standley & Williams (1963, p. 530) stated that it was widely cultivated for ornament in Guatemala, especially in the central highlands around Cobán, where panicles of flowers were often sold in markets.

For a long time *Fuchsia boliviana* was incorrectly called *F. corymbiflora* and the species was not actually named until 1876. It was probably introduced into Central America and Mexico in the mid-1800s. Since it requires so little care and flowers throughout the year, *F. boliviana* is a very popular garden shrub in many villages, where it often becomes locally naturalized.

Fuchsia hybrida and *F. magellanica* are both more recent introductions into the area and do not occur outside of cultivation as far as we know.

There are probably no plants of the rare, epiphytic and tuberous *Fuchsia decidua* alive in cultivation today. It has been cultivated within the last 15 years in Mexico, California, and Great Britain, and a cultivar distributed as "President Gosselin" in horticultural circles in the United States and Britain in approximately the past 30 years might have been *F. decidua,* but we cannot verify this because we have seen no specimens or living plants.

Key to the Species of *Fuchsia* in Mexico and Central America

1a. Flowers borne in racemes or panicles.
  2a. Flowers erect, numerous, in terminal, di- to trichotomously branched panicles (sect. *Schufia*).
    3a. Leaves entire, smooth, 10–21 cm long; hermaphroditic; floral tube obconic, with flowers widening toward the apex in bud; anthers oblong, mostly ca. 2 mm long; style always exserted beyond the anthers, the stigma four-lobed, each lobe ca. 1.5 mm long. Mexico, Durango to Oaxaca. ---------- 5. *F. arborescens*
    3b. Leaves minutely to coarsely serrate, ridged, 5–15 cm long; gynodioecious (functionally subdioecious), with hermaphroditic populations north of the Isthmus of Tehuantepec; floral tube cylindric to narrowly obconic, not much widened above in bud; perfect flowers with ovoid-reniform anthers less than 2 mm long, generally ca. 1 mm; style exserted beyond or held below the anthers, stigma four-lobed to strongly reduced; pistillate flowers smaller, the anthers abortive, the stigma exserted and four-lobed. Mexico to Panama. ---------- 6. *F. paniculata*
  2b. Flowers pendulous to spreading in simple racemes or few-branched panicles.
    4a. Floral tube less than 6 mm long; antipetalous stamens reflexed and included in the tube (sect. *Jimenezia*). ---------- 4. *F. jimenezii*

4b. Floral tube more than 30 mm long; all stamens erect.
5a. Flowers in compact, lateral panicles; petals much reduced, less than 3.5 mm long; flowering when leafless. ---------- 3. *F. decidua* (sect. *Ellobium*)
5b. Flowers in terminal, drooping racemes; petals more than 6 mm long; flowering with leaves.
6a. Plants often with tubers; leaves ovate to cordate; sepals ascending to spreading, greenish; stigma green. ---------- 2. *F. fulgens* (sect. *Ellobium*)
6b. Plants without tubers; leaves elliptic to ovate; sepals initially spreading, then strongly reflexed, red; stigma cream. Introduced. ---------- 7. *F. boliviana* (sect. *Fuchsia*)

1b. Flowers axillary, not in a definite inflorescence.
7a. Antipetalous stamens reflexed and included in the tube; berry few-seeded (6–36); subdioecious to dioecious. ---------- sect. *Encliandra* (see Breedlove, 1969)
7b. Antipetalous stamens erect and exserted above the rim of the tube; berry many-seeded (>50); hermaphroditic.
8a. Sepals shorter than the tube; petals green, 6–12 mm long. ---------- 1. *F. splendens* (sect. *Ellobium*)
8b. Sepals mostly longer than the tube; petals showy, 10–20 mm long, never green. Cultivated. (sect. *Quelusia*).
9a. Tube 5–10 mm long, sepals 15–25 mm long, petals purple. ---------- *F. magellanica* Lam.[5]
9b. Tube 10–20 mm or more long, sepals generally 25–30 mm long; variable garden hybrids. ---------- *F. hybrida* Hort.[5]

Fuchsia sect. **Ellobium** (Lilja) Breedlove, Berry, & Raven, **comb. nov.** *Ellobium* Lilja, Linnaea 15:262. 1841. TYPE: *Fuchsia fulgens* De Candolle; based on *Spachia* Lilja; non *Ellobum* Blume, 1826, nom. rejic.

Spachia Lilja, Tidning Trädgårdsskötsel allmän Wextkultur 8:62. 1840, hom. illeg., non *Spachea* Juss. 1838.

Hermaphroditic. Soft wooded, terrestrial, or epiphytic shrubs, some species tuberous. Leaves opposite or ternate, membranous, elliptic-ovate to cordate. Flowers axillary, racemose, or paniculate. Floral tube longer than sepals. Petals usually ½ length of the sepals or less. Nectary unlobed, a smooth band 0.3–0.5 mm thick lining the base of the floral tube. Stamens biseriate, erect, shorter than the sepals or exserted less than 5 mm beyond them, the antisepalous stamens longer than the antipetalous ones. Stigma green. Berry ellipsoid to narrowly cylindric; seeds ca. 50–ca. 200, laterally compressed, oblong to irregularly triangular in outline, 1–2 mm long, 0.5–1.5 mm wide. Gametic chromosome number $n = 11$.

Distribution: Evergreen cloud forests and moist oak-pine forests from northern Costa Rica to Jalisco, Mexico, at altitudes of 1,450–3,400 m (Figs. 1 and 2).

Munz (1943) placed *Fuchsia splendens* (including *F. cordifolia*) and *F. fulgens* in the large, generalized sect. *Fuchsia*. *Fuchsia decidua* was included in sect. *Hemsleyella*, a smaller South American group with tubers, apetalous flowers, and often an epiphytic, dry season flowering habit. Geographically and morphologically, however, the three species of sect. *Ellobium* form a well defined group that does approach the above mentioned sections in several characters, but can be distinguished by the characters shown in Table 1.

[5] See appendix for lists of specimens examined from Mexico and Central America.

FIGURE 1. Distribution of *Fuchsia splendens* (sect. *Ellobium*).

The species in sect. *Ellobium* follow a clear progression of specialization from *F. splendens,* the most generalized, to *F. decidua,* the most specialized. This progression consists of a reduction in petal size, change in flower position from axillary to racemose to paniculate, and the development of tubers and an epiphytic habit in *F. fulgens* and *F. decidua,* accompanied by a marked seasonality in the phenology of flowers and leaves. Furthermore, *F. splendens* is the most widespread species, and *F. decidua* is rare.

1. **Fuchsia splendens** Zuccarini, Flora 15, ii, Beibl., 102. 1832. TYPE: Los Molinos, Oaxaca, Mexico, 1827–1832, *Wilhelm Karwinsky* (M, holotype; photographs, F, GH, MICH, MO, POM, US; BR, G, isotypes). Lindl., Bot. Reg. 28:*pl. 27.* 1842. Curtis, Bot. Mag. 70:*pl. 4082.* 1844. Planch., Fl. Serres Jard. Eur. 5:*t. 458.* 1849. Watson, Garden 55:74, *fig.* 1899. Hemsl., Gard. Chron. 3(45):338, *t.* 1909. Standl., Contr. U.S. Natl. Herb. 23:1078. 1924. Munz, Proc. Calif. Acad. Sci. IV. 25:20, *pl. 1, fig. 6.* 1943. Standl. and Williams, Fieldiana, Bot. 24(7):534, *fig. 85.* 1963. Munz, N. Am. Flora II. 5:4. 1965. Chickering, Flowers of Guatemala 64, *pl. 18.* 1973.

Fuchsia cordifolia Bentham, Pl. Hartw. 74. 1841. TYPE: Near summit of Volcán Santa María ("Xetuch"), ca. 3,000 m, Quezaltenango, Guatemala, Nov. 1839, *Theodor Hartweg 528* (K Bentham Herb., holotype; photograph, MO; BM, CGE, G, K Hooker Herb., LE, OXF, P, U, W, isotypes). Harrison, Floric. Cab. and Florist's Mag. 9:241, *pl.* 1841. Lindl., Bot. Reg. 27, *pl. 70.* 1841. Hook., Icon. Pl. 5:*t. 450.* 1842. Essig, Nat. Hort. Mag. 13:6, *photo.* 1934. Munz, Proc. Calif.

FIGURE 2. Distribution of *Fuchsia decidua*, *F. fulgens* (sect. *Ellobium*) and *F. jimenezii* (sect. *Jimenezia*).

Acad. Sci. IV. 25:21. 1943. Standl. and Williams, Fieldiana, Bot. 24(7):530. 1963. Munz, N. Am. Flora II. 5:5. 1965.

Fuchsia intermedia Hemsley, Diag. Pl. Nov. Mex. Centr. Amer. 1:14. 1878. TYPE: Summit of Mt. Totontepec, 3,000 m, Oaxaca, Mexico, April 1839, *Theodor Hartweg 460* (K, holotype; photograph, MO; BM, CGE, LE, OXF, P, W, isotypes). Standl., Contr. U.S. Natl. Herb. 23:1078. 1924.

Few- to many-branched, soft-wooded shrub 0.5–2.5 m tall, terrestrial or occasionally epiphytic on trees. Branchlets 0.5–3 dm long, 1–3 mm thick, triangular to quadrangular, subglabrous to densely short-pilose or villous; older branches with smooth reddish bark, exfoliating freely with age, 0.5–3 m long and 8–40 mm thick. Leaves opposite or occasionally ternate, membranous, ovate to cordate, rounded to cordate at base, acute to acuminate at apex, 35–130 mm long, 20–75 mm wide, pale to dark green and subglabrous to pilose or villous above, lighter below or red tinged and similarly pubescent, especially along nerves; secondary veins 5–9 on either side of the midvein, margin dentate to serrate; petioles reddish, pubescent, 12–80 mm long; stipules lance-filiform, 1–2 mm long, ca. 0.3 mm wide, deciduous. Flowers axillary and solitary in upper leafy nodes of the year's branches; pedicels spreading to drooping, slender, subglabrous to strigose, 35–75 mm long; ovary narrowly cylindrical; floral tube narrowly to broadly cylindric, 20–46(–64) mm long, 4–9 mm wide and usually ventricose and laterally compressed at the base around the nectary, ± dilated in upper half, 5–15 mm wide at the rim, pubescent or with glandular hairs outside, subglabrous or loosely strigose inside in lower ½; sepals lanceolate, 8–20 mm long, 5–8 mm wide, spread-

TABLE 1. Comparison of sects. *Ellobium*, *Fuchsia*, and *Hemsleyella*.

Section	Presence of Petals	Presence of Tubers	Type of Nectary[1]	Epiphytism	Distribution
Ellobium	Yes	2 of 3 spp.	Band	Yes	Mexico, Central America
Fuchsia	Yes	None	Ring	No	Tropical Andes and Hispaniola
Hemsleyella	No	Most species	Band	Yes	Tropical Andes

[1] Band nectary is smooth and fully adnate to the floral tube; ring nectary is annular and mostly free from the tube. Three of the approximately 60 species in sect. *Fuchsia* have nectaries adnate to the tube, but they are variously lobed.

ing at anthesis; tube rose to bright red, sepals green with reddish base; petals olive green, ovate, 6–12 mm long, 4–8 mm wide, rounded to cordate at the base, subacuminate at the apex, erect; nectary a lustrous yellow band ca. 0.4 mm thick lining the basal 4–8 mm of the tube; stamens exserted beyond petals; filaments pale yellow green, the antisepalous ones 10–20 mm long, the antipetalous ones 6–14 mm long and inserted on the tube ca. 1 mm below the insertion of the petals; anthers oblong, yellow, 2–3 mm long, 1–2 mm wide; style glabrous, pale green, 40–76 mm long; stigma green, subconic, 2–3 mm long, 1–2 mm wide, 4-parted at the apex. Berry elongate, 20–40 mm long, 5–8 mm thick, verrucose, green to dark purple when ripe; seeds 1.5–2 mm long, ca. 0.5 mm thick. Gametic chromosome number, $n = 11$.

Distribution: Mexico to Costa Rica. Scattered in a few moist forest localities in Guerrero and Oaxaca, more common in cloud forest and moist oak-pine forest from Chiapas to Costa Rica, 2,000–3,400 m (Fig. 1). Flowering throughout the year.

Representative specimens examined: MEXICO, CHIAPAS: San Cristóbal las Casas, NE side of Zontehuitz, *Breedlove 7799* (BM, DS, GH); ca. 2 km W of Nabenchauck, municipio Zinacantán, *Breedlove 7493* (DS, GH); N & W slopes of Cerro Mozotal, road from Huixtla to Siltepec, *Breedlove 25858* (MO); Cerro Huitepec, *Ghiesbreght 698* (GH, K, LE, MO); Chamula, *Linden 675* (G, K, LE); La Cola del Diablo, ca. 20 km N of San Cristóbal Las Casas, *Luteyn 3566* (DUKE); Mt. Tacaná, *Matuda 2322* (GH, NA, K); Motozintla, Pinabeto, *Matuda 15466* (F, IPN, LL). GUERRERO: Pie de la Cuesta-Toro Muerto, *Hinton et al. 11222* (GH, K, NY, US); Cerro Teotepec, *Rzedowski & McVaugh 184* (DS, ENCB, MICH, TEX); Tlacotepec, *Paray 2012* (ENCB); Piedra Ancha, Galeana district, *Hinton et al. 14223* (GH, MICH, NY, US). GUATEMALA, CHIMALTENANGO: Chichoy Pass, *Hunnewell 14675* (GH); Volcán Acatenango, *Hunnewell 14766* (GH); Cerro de Tecpam, *Standley 61000* (A). EL PROGRESO: between Finca Piamonte and Volcán Santa Luisa, *Steyermark 43567* (BH). HUEHUETENANGO: Cerro Pixpix, above San Idelfonso Ixtahuacán, *Steyermark 50642* (BH); Cruz de Limón, between San Mateo Ixtatán and Nucá, *Steyermark 49814* (BH); San Juan Ixcoy, Cordillera de los Cuchumatanes, *Steyermark 50046* (BH). JALAPA: Montaña Miramundo, *Steyermark 32833* (F). JUTIAPA: Asunción, Mita, Volcán Suchitán, *Steyermark 31944* (F). QUEZALTENANGO: Cerro Quemado, *Kellerman 5935* (LL, US); Cuesta de El Caracol, 5–8 km N of San Juan Ostuncalco, *Williams et al. 22777* (G, S, W); Volcán Santa María, *Skutch 867* (A, BM, G), *Skinner s.n.* (K); Volcán Zunil, *Steyermark 34686* (F, US). QUICHÉ: Chiul, *Heyde & Lux 1890* (GH, MO); above Nebaj toward Acatenango, *Hunnewell 14776* (GH). SACATEPÉQUEZ: Volcán de Agua, *Donnell Smith 2174* (F, GH, M, NY, PH). SAN MARCOS: San Luis, ca. 6 km W of Ixchiguán, *Beaman 3243* (DUKE); San Sebastián, Volcán Tajulmulco, *Steyermark 35844* (F, NY). SOLALÁ: Volcán San Pedro, N slopes, *Steyermark 47260* (BH); Volcán Atitlán, *Steyermark 47526* (F, G); ca. 18 km SE of Totonicapán, *Webster et al. 11760* (MO); Cerro Metía Tecum, 5–10 km S of Los Encuentros, *Williams et al. 41729* (BM, MICH). TOTONICAPÁN: Between Los Encuentros and Totonicapán, *Bunting 1302* (F); ca. 13 km S of Totonicapán, *Williams et al. 22909* (G). EL SALVADOR, CHALATENANGO: summit of

Los Esemiles, *Tucker 1116* (BH, G, LL, MICH, NY, PH). SANTA ANA: Cerro Montecristo, *Allen 7154* (F, GH, LL, NY, US). COSTA RICA, CARTAGO: near Ojo de Agua camp, *Dayton 3029* (F, MO); Villa Mills, *Holm & Iltis 516* (A, BM, F, G, MO, NY), *Raven 22051* (DS); Cerro Sákira at La Asunción, *Wilbur & Stone 10036* (DUKE). SAN JOSÉ: Cerro de la Muerte, *Burch 4716* (DUKE, MO); trail from Canaan to Chirripó via Los Angeles, N of Río Talari, *Burger & Liesner 7396* (F, S); Cordillera de Talamanca, Pacific slopes of Chirripó massif, *Davidse & Pohl 1619* (MO); Cerro de la Vueltas, *Pittier 10501* (BR, G, US); 5 km SE of La Asunción, before La Georgina, *Wilbur 14386* (DUKE, MO); 9 km NW of La Asunción, *Wilbur 14407* (DUKE).

Cultivated specimens: AUSTRIA, Vienna, 1903 (W). ECUADOR, PINCHINCHA: Hacienda Cataguango, W of Amaguaña, 1976, *Ortiz s.n.* (QCA). GERMANY, Berlin, 1905, *Bothe s.n.* (B). GUATEMALA, Guatemala City, 1947, *Brenckle 47-431* (NY). IRELAND, Dublin Botanical Garden, 1844 (K). SOVIET UNION, Leningrad, 1845 (LE). UNITED STATES, CALIFORNIA: Berkeley, *Hutchison 54.522.* (UC).

This species is unique in its elongate ovary and fruits, green petals, and ventricose, laterally compressed base of the floral tube. The peculiar compression of the floral tube has been well illustrated in horticultural journals; e.g., by Planchon (1849) and Hemsley (1909).

Fuchsia splendens has the widest range in sect. *Ellobium,* from Costa Rica to Guerrero, Mexico. Variation in leaf shape is considerable, but it is mostly related to the degree of development of the leaf. On the same individual, the young upper leaves are often ovate while the lower ones are cordate. Pubescence varies to a much greater extent, with densely villous hairs on *Linden 657* (G, K, LE; from Chiapas); glandular hairs on *Breedlove 9347* (BM, GH; also from Chiapas); finely pubescent hairs or even subglabrous plants in most Costa Rican collections. The most variable character of all is floral tube dimensions. Differences in floral tube lengths were used to describe *F. cordifolia,* longer-tubed than *F. splendens,* and *F. intermedia,* of intermediate length. Field studies and analysis of herbarium specimens have shown no geographic or ecological pattern to this variation, however. The type of *F. cordifolia* has floral tubes ca. 40 mm long; the type of *F. splendens* has floral tubes ca. 25 mm long. This does not nearly cover the variation found, however, since *Skutch 867* (A, BM, G), from Volcán Santa María in Guatemala, has floral tubes to 64 mm long. *Skinner s.n.* (K) is from the same mountain at a similar elevation, yet it has floral tubes only 20 mm long. In view of this variation and the presence, throughout the range, of the common assemblage of unusual characters mentioned above, we are including both *F. cordifolia* and *F. intermedia* as synonyms of *F. splendens.*

Diploid gametic chromosome counts of $n = 11$ were obtained from *Breedlove 7796* (DS) and *Raven 22051* (DS). Both Bentham (1841, p. 74) and Standley & Williams (1963) noted that inhabitants of the Volcán Santa María area called this species "Melocotoncito" (little peach). Hunters in that area would commonly rely on the conspicuous, epiphytic bushes of *F. splendens* for their sour, juicy fruits when water was not available.

2. **Fuchsia fulgens** De Candolle, Prodr. 3:39. 1828. TYPE: Plate 362 of Sessé & Mociño's Flora Mexicana Icones, ined. (Copy at G). The collection of illustrations made in Mexico by the Expedición Real de Botánica was lent by Mociño to A. De Candolle in 1813. These were copied by De Candolle in Geneva when Mociño requested their return in 1817 on very short notice (Sprague, 1926). De Candolle later went on to describe some 270 new species

from these illustrations, including *F. fulgens*. Plate 362 undoubtedly corresponds to the specimens collected by Sessé et al. and used to describe *F. racemosa* Sessé & Mociño (= *F. fulgens*); the type locality for *F. fulgens* is therefore the same as for *F. racemosa* (in the mountains of Pátzcuaro, Michoacán, Mexico). Lindl., Bot. Reg. 24:*t. 1*. 1838. Curtis, Bot. Mag. 67:*t. 3801*. 1840. DC., Calques Dessins Mociño Sessé 1:*pl. 362*. 1874. Raimann in Engl. & Prantl, Nat. Pfl. 3(7):200, *fig*. 1893. Watson, Garden 55:75, *fig*. 1899. Standl., Contr. U.S. Natl. Herb. 23:1078. 1924. Essig, Nat. Hort. Mag. 13:9, *photo*. 1934. Munz, Proc. Calif. Acad. Sci. IV. 25:55, *pl. 8, fig. 43*. 1943. Chittenden, Dict. Gard. 2:846, *fig*. 1951. Munz, N. Am. Flora II. 5:6. 1965. Morley & Everard, Wild Flowers of the World, *pl. 173, fig. F1*. 1970. *Spachia fulgens* (DC.) Lilja, Tidning Trädgårdsskötsel allman Wextkultur 8:62. 1840. *Ellobium fulgens* (DC.) Lilja, Linnaea 15:262. 1841.

Fuchsia fulgens pumila Carrière, Rev. Hort. 53:150, 1881. TYPE: Rev. Hort. 53:150, *plate*, 1881. No specimens of this entity were seen. The plant illustrated is from garden material of unspecified origin, cultivated in France ca. 1881.

Fuchsia racemosa Sessé & Mociño, Pl. Nov. Hisp. 58. 1888; non Lamarck, 1788. TYPE: On boulders in the mountains of Pátzcuaro, Michoacán, Mexico, Sept. 1790, *Martín Sessé, José Mociño, Juan Diego del Castillo & José Maldonado 5211* (MA, lectotype here designated. A second sheet of *F. fulgens* at MA has a Ruiz & Pavón label, but it is probably a duplicate of the type material). Fl. Mex. 101. 1893.

Soft-wooded shrubs 0.5–3 m tall, with thickened, tuberous underground parts, often epiphytic in trees or on rocks. Branchlets 4–25 cm long, 1–5 cm thick, semi-succulent, quadrangular, subglabrous to strigose, reddish; older branches and stems freely exfoliating, 1–6 cm thick. Leaves opposite, soft-membranous, ovate to cordate, rounded to cordate at base, acute at apex, (5–)9–15 cm long, (3–)5–12 cm wide, pale green above, lighter below and red-tinged; young leaves canescent to tomentose, the older ones short villous; secondary veins 8–10 on either side of the midvein, margin denticulate to serrulate with red glandular teeth; petiole stout, strigose, 3–8 cm long; stipules subtuberculate, lance-deltoid, 1.2–2 mm long, 0.2–0.5 mm wide, deciduous. Flowers several to many in terminal, drooping racemes, the rachis 3–20 cm long; bracts reflexed, ovate to elliptic, 0.5–2.5 cm long; pedicels slender, strigose, 10–20 mm long; ovary cylindrical, 12–15 mm long, 3–4.5 mm thick, strigose; floral tube narrowly funnelform, 50–65 mm long, 2–4 mm wide at the base, gradually widened above until 7–10 mm wide at the rim, loosely villous outside and inside; sepals lanceolate, subacuminate, 12–17 mm long, 4–6 mm wide, spreading or suberect at anthesis; tube pink to dull red, sepals pale red and yellow green towards the apex; petals bright red, elliptic to ovate, 6–9 mm long, 4–6 mm wide, rounded at base, acute at apex, erect; nectary a smooth yellow green band 0.3–0.4 mm thick lining the basal 3–5 mm of the tube; filaments light red, the antisepalous ones 9–10 mm long, the antipetalous ones 5–7 mm long; anthers white, 2.5–3 mm long, 1–2 mm thick; style slender, pink, pubescent in lower ½, 60–82 mm long; stigma green, subconic, 2–3 mm long, ca. 1.5 mm thick. Berry elongate, 20–30 mm long, 8–15 mm thick, glabrous to sparsely strigillose, dark purple; seeds 1–1.5 mm long, ca. 1 mm thick, ovate to subtriangular in outline. Gametic chromosome number, $n = 11$.

Distribution: Mexico. Mostly epiphytic, in oaks or on rocks, especially around

seepages and waterfalls along the Trans-Mexican Volcanic Belt from Jalisco to the State of Mexico and in the Sierra Madre Occidental of Guerrero, 1,450–2,300 m (Fig. 2). Flowering in the wet season, June through September.

Representative specimens examined: MEXICO, GUERRERO: Omiltemi, 60 km W of Chilpancingo, *Rowell 3047* (MICH), *Tillett 637-150* (DS, GH). JALISCO: Huejotitán, *Diguet s.n.* (S); E slopes of Volcán Colima, *Goldsmith 22* (DS, F, GH, MO, NY, UC, US); Zapototán de Hildalgo, S of Guadalajara, *Gregory & Eiten 230* (MICH, MO); San Juan Cosalá, *Villarreal de Puga 28* (IPN); 10–15 km S of Autlán, *Wilbur & Wilbur 1438* (DUKE); E of Manantlán, ca. 22 km S-SE of Autlán, *Wilbur & Wilbur 1816* (DUKE). MEXICO: Amanalco, Valle de Bravo, *Dressler 2433* (US); Tequexquipan, Temascaltepec District, *Hinton 823* (BM, K); Rincón del Carmen, Temascaltepec District, *Hinton 1744* (BM, G, GH, K); Salitre-Cañitas, *Hinton et al. 4311* (BM, G, K); Comunidad, Temascaltepec District, *Hinton 4894* (A, BM, K); Ipericones, Temascaltepec District, *Hinton 3893* (K), *Hinton et al. 8071* (DS, GH, K, MICH, NY, U); Nanchititla, *Matuda et al. 30368* (GH, MEXU). MICHOACÁN: Km 16 of Uruapan-Los Reyes road, *Beaman 2418* (GH); 26 km E of Morelia, *Breedlove 7726* (DS); NW of Uruapan at San Juan Nuevo, *Breedlove 15776* (BM, DS); near Morelia, *Hartweg 286* (CGE, G, K, LE, OXF, W); Zitácuaro, *Hinton et al. 11883* (GH, K); S of Torricillas, Coalcomán District, *Hinton 13987* (H, NA, PH); S of Naranjillo, *Hinton et al. 13952* (PH); Tancítaro, *Leavenworth 303* (F, GH, MICH, MO, NY); Paracho, km 47–48 of Guadalajara-Uruapan road, *Moore & Wood 4050* (A, BH, GM, DUKE, MICH); Pátzcuaro, *Pringle 4123* (BH, BM, G, GH, K, LE, MO, PH, S, W, Z); Tarascón, *Pringle 11988½* (BH, GH, K).

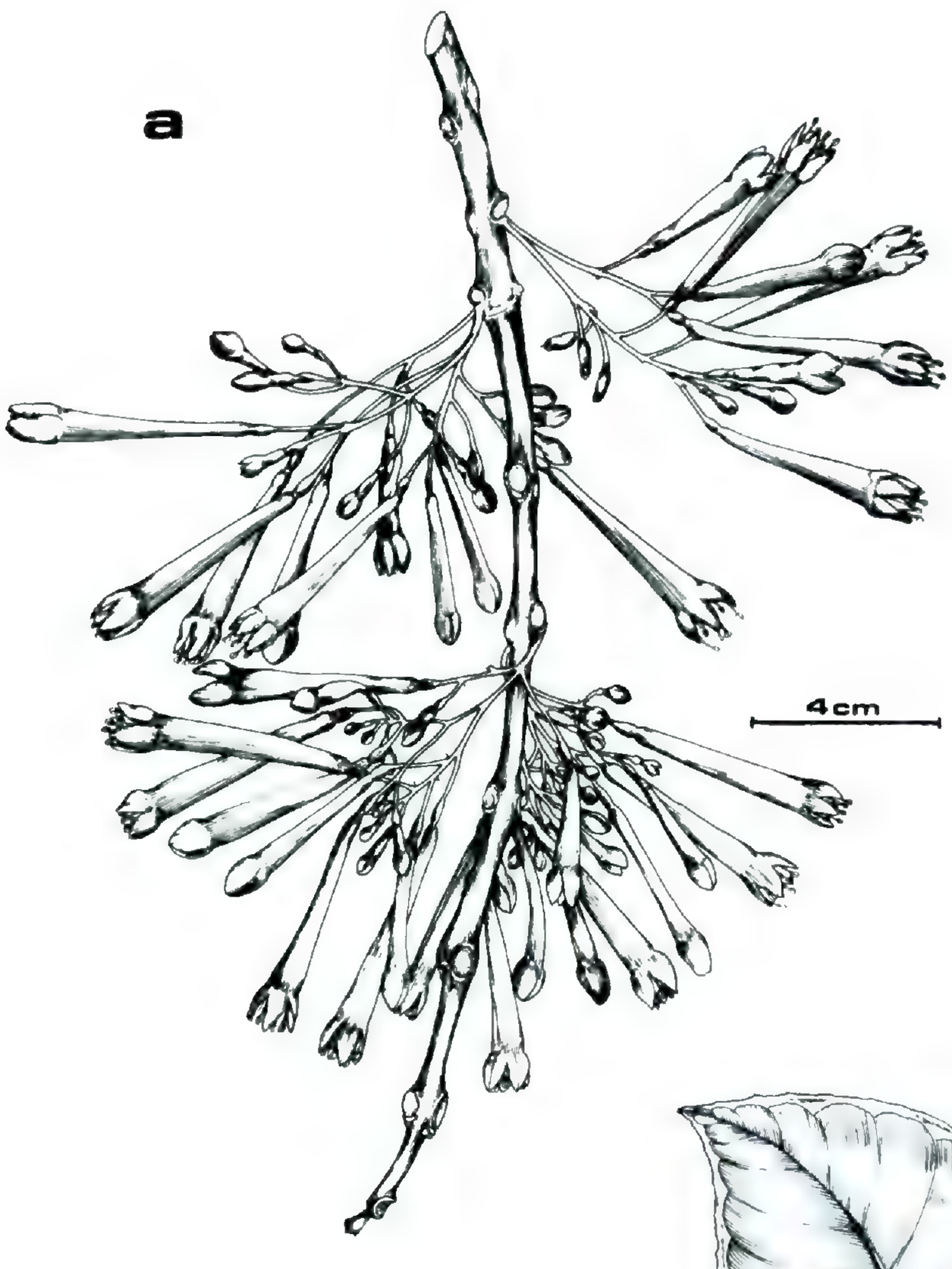
Cultivated specimens: AUSTRIA, Vienna, 1849 (W). FRANCE, Nantes, 1839 (BM); Paris, 1843 (P). GERMANY, Munich, 1843 (BR); Heidelberg, 1923 (BH); Berlin, 1966, *R196* (B). GREAT BRITAIN, 1836–1843, *Saul s.n.* (NA). MEXICO, VERACRUZ: Jalapa, 1881, *Kerber s.n.* (W). SOVIET UNION, Leningrad, 1840 (LE). UNITED STATES, CALIFORNIA: Berkeley, 1965, *Hutchinson 49.803.1* (UC, NA); Santa Barbara, 1910, *Popenoe 618* (NA).

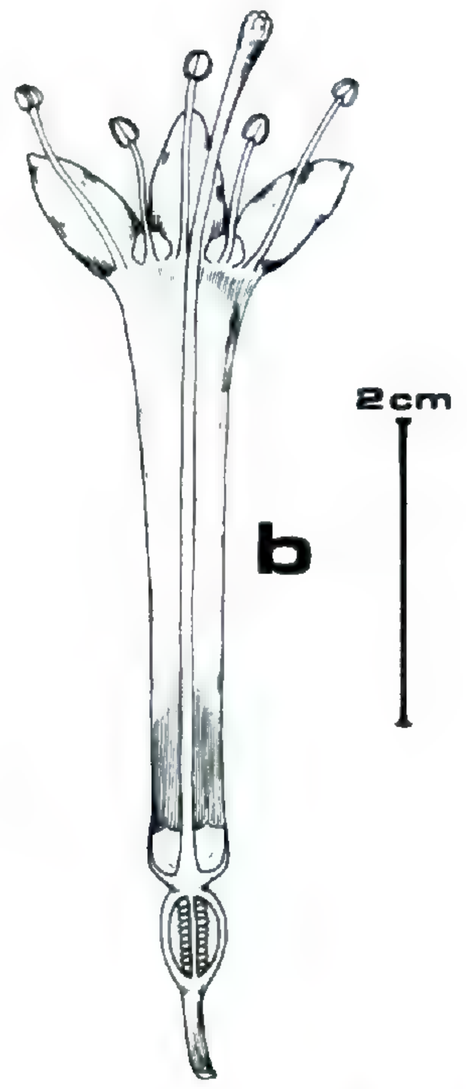
The long-tubed, many-flowered racemes of *Fuchsia fulgens* resemble those of South American species such as *F. boliviana* and *F. dependens*. It is easily distinguished from these species, however, by the presence of tubers, the occasionally epiphytic habit, the cordate leaves, and the greenish sepals and stigma. It is sympatric with *F. decidua* in Jalisco and Guerrero, but *F. decidua* flowers when leafless in the dry season (December–May), and *F. fulgens* flowers with leaves in the rainy season (June–November). Both *Hinton 3893* (K) and *Hinton et al. 11883* (GH, K) were collected in May and are unusual in having just a few young expanding leaves at the shoot apices and flowers borne on dense racemes from the axils of older leafless branches, much like *F. decidua*.

Diploid gametic chromosome counts of $n = 11$ were obtained from *Breedlove 15776* (BM, DS) and *Hutchison 49-803* (UC).

3. **Fuchsia decidua** Standley, Publ. Field Mus. Bot. 4:248. 1929. TYPE: La Bufa, Real Alto, Sierra Madre Occidental, 2,500 m, Jalisco, Mexico, 30 January 1927, *Ynes Mexia 1601* (F 579815, holotype; A, BM, C, CAS, DS, G, MICH, MO, NY, UC, US, Z, isotypes). Munz, Proc. Calif. Acad. Sci. IV. 25:75, *pl. 12, fig. 75.* 1943, N. Am. Flora II. 5:7. 1965.—FIG. 3.

Shrub 0.5–2 m high, terrestrial, in rock crevices, or epiphytic in trees as high as 10 m above the ground, with fleshy tubers 2–4 cm thick and stoloniferous lateral shoots. Branchlets 5–15 cm long, 3–6 mm thick, subquadrangular, glabrous; older branches 0.5–ca. 3 m long, 6–20 mm thick, with very loosely peeling, copper brown bark. Leaves opposite, chartaceous, elliptic to ovate-cordate, cuneate to cordate at base, acute to acuminate at apex, 9–17 cm long, 5–8 cm wide, sparsely strigillose above, glabrous below; margin subentire to denticulate; deciduous, leafy in the wet season (June–November); petiole glabrous to strigillose,





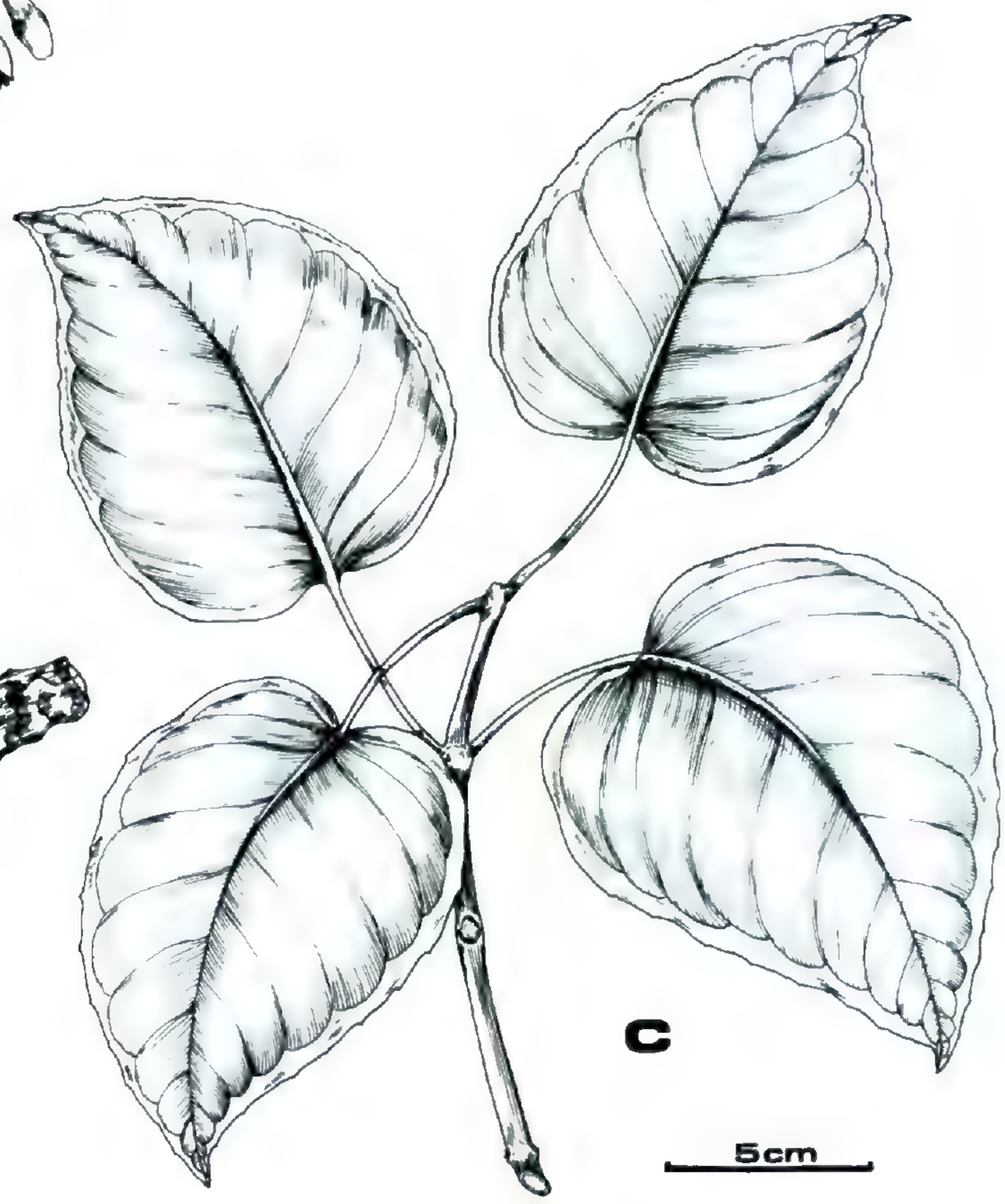


FIGURE 3. *Fuchsia decidua* Standley.—a. Inflorescence.—b. Flower, longitudinal section. a & b from *McVaugh 26157* (MICH), Jalisco, Mexico.—c. Leaves. From *MacDougall H.521* (MO), Oaxaca, Mexico.—d. Tuber. From *Mexia 1061* (A), Jalisco, Mexico.

3–5 cm long; stipules triangular, 1–1.5 mm long, ca. 0.5 mm wide, deciduous. Flowers numerous in compact, lateral panicles on new shoots arising from the nodes of older stems, the rachis 2–6 cm long, drooping, flowering when leafless (December–May); pedicels slender, glabrous, 6–11 mm long, to 15 mm in fruit;

floral tube narrowly funnelform, 30–48 mm long, 1.5–3.5 mm wide at base, then slightly constricted above nectary and gradually widened above until 5–9 mm wide at rim, glabrous to sparsely strigose outside, glabrous within; sepals lance-oblong, 8–13 mm long, 3–6 mm wide, apex obtuse, spreading to suberect at anthesis; tube and sepals reddish pink; petals red, fleshy, oval to reniform, 1.5–3.5 mm long, 1.5–4 mm wide, erect; nectary a smooth yellow green band 3–5 mm high lining the base of the tube; antisepalous filaments 10–17 mm long, antipetalous filaments 5–12 mm long; anthers 1.5–3 mm long, 1–2 mm wide; style slender, 55–66 mm long; stigma green, slender, 1–1.5 mm long, ca. 1 mm thick. Berry ellipsoid, 8–12 mm long, 4–6 mm thick, glabrous, greenish purple; seeds 1.5–2 mm long, 0.5–1.0 mm thick, ovate in outline. Gametic chromosome number, $n = 11$.

Distribution: Mexico. Rare shrubs and epiphytes in moist oak-pine and evergreen cloud forests in the Sierra Madre Occidental from Jalisco to Oaxaca (Fig. 2). Flowering in the dry season (December–May).

Specimens examined: MEXICO, GUERRERO: Omiltemi, ca. 60 km W of Chilpancingo, *Breedlove 15821* (DS, LL), *Lachica s.n.* (IPN); W of Filo de Caballo, *Breedlove 15829* (DS); Highway 95 ca. 6 km W of turnoff to Chichihualco, *Croat 45630* (MO); Cerro Alquitrán, *Kruse s.n.* (DS); Chichihualco, Camotla, Cerro de la Pastilla, *Rzedowski 16435* (IPN, MICH); Campamento El Gallo, *Rzedowski & McVaugh 189* (DS, MICH). JALISCO: Sierra de Manantlán, above Durazno, *Boutin 3036* (MO); Mesa de los Gallos, *González 843* (MO); SSE of Autlán, SE of Ahuacapán, *McVaugh & Koelz 918* (MICH); SE of Autlán, trail from Chante, above Rancho Manantlán, *McVaugh 10295* (MICH); near Santa Mónica, *McVaugh 14047* (MICH); Autlán, Sierra de Manantlán, between El Chante and Cuzalpa, *McVaugh 23100* (IPN, MICH); Ayutla, San Miguel de la Sierra, *McVaugh 23500* (MICH); Sierra de Manantlán, 25 km S of El Chante, *McVaugh 26157* (MICH). OAXACA: S of Tlaxiaco, San Andrés Chichahuastla, Cerro Zarzamora, *MacDougall H.521* (MO), *s.n.* (US).

Cultivated specimens: MEXICO, DISTRITO FEDERAL: Mexico City, *Kruse in 1967* (DS). OAXACA: Oaxaca, *MacDougall 468* (US).

The tiny, thick petals and leafless, dry-season flowering distinguish *Fuchsia decidua* from the related *F. fulgens* and *F. splendens*. The habit of *F. decidua* is unusual and is shared only by some members of the South American sect. *Hemsleyella*. *Fuchsia decidua* grows epiphytically, mostly on the trunks of oaks, but also terrestrially on rocks. Plants with thick, fleshy, prostrate stems ca. 2 cm thick extending up to nearly 3 m long are rooted in moss and rich humus (F. Boutin, T. MacDougall, pers. comm.). This species is well adapted to the rather seasonal climate of the areas in which it occurs. The tubers store food and water during the wet season, when the plants are leafy and actively growing vegetatively. In the dry season, the plants are deciduous and flower on stems from the previous season's growth. The seeds are apparently spread by birds from tree to tree and from cliff to cliff. A single somatic chromosome count of $2n = 22$ was obtained from *Breedlove 15821* (DS).

Fuchsia sect. **Jimenezia,** Breedlove, Berry & Raven, **sect. nov.** TYPE: *Fuchsia jimenezii* Breedlove, Berry & Raven.

Hermaphroditicus. Folia opposita ellipticaque. Flores racemosi vel interdum paniculati; nectarium disco annulari styli basin cingens et basin tubi adnatum; stamina inaequalia, filamentis antisepalis erectis et supra tubum exsertis, antipetalis in tubum reflexis inclusisque. Bacca subglobosa, seminibus multis, compressis.

Hermaphroditic. Glabrous shrubs. Leaves opposite, elliptic to lance-elliptic. Flowers in terminal racemes or few-branched panicles. Floral tubes less than 5 mm long, shorter than sepals or petals. Nectary annular, irregularly 4-lobed, adnate to the tube. Stamens biseriate, the antisepalous stamens erect, the antipetalous stamens reflexed and included in the tube. Berry subglobose; seeds many, ca. 50–ca. 100, laterally compressed, 0.9–1.2 mm long, 0.5–0.7 mm wide. Gametic chromosome number, $n = 11$.

4. Fuchsia jimenezii Breedlove, Berry & Raven, **sp. nov.**—TYPE: Monte verde, exposed crest of the Sierra de Tilarán, Puntarenas, Costa Rica, 23 June, 1967, *Thomas Emmel* (DS 614763, holotype; BM, CAS, ENCB, F, GH, K, LE, LL, MICH, NT, RSA, US, isotypes). This species is dedicated to Alfonso Jiménez Muñoz, a long time student of the Costa Rican flora, who first called this entity to our attention as an undescribed species in 1967. FIG. 4.

Fuchsia arborescens sensu Woodson & Schery, Ann. Missouri Bot. Gard. 46:328. 1959, pro parte.

Frutex erectus vel scandens 0.4–2.0 m altus, omnino glaber; rami ad 3 cm crassi cortice subtiliter fissurato. Folia opposita, subcoriacea, elliptica vel lanceo-elliptica, (3–)6.5–11.5 cm longa, 2.5–4.8 cm lata. Flores racemosi vel interdum paniculati, racemo 5–20 cm longo; pedicelli erecti vel divergentes, tenues, 6–12 mm longi, fructu ad 18 mm longo; tubus floralis subcylindricus vel subobconicus, 2.5–4.5 mm longus, apice 2–4.5 mm latus, basi 1.5–2.5 mm latus; sepala late lanceolata, 4–6 mm longa, basi 2.5–3.5 mm lata, divergentes; tubus sepalaque rubra vel roseo-rubra; petala rosea, suborbicularia vel ovata, 4–6 mm longa, 3–4 mm lata, basi rotundata, apice rotundata vel acuta, erecta; discus annularis lobis plerumque quattuor vel pluribus supra basin tubi 1–1.5 mm elevatus; filamenta antisepala 1–2 mm longa erectaque, antipetala 0.8–1.5 mm longa, in tubum reflexa inclusaque, antherae 1.5–2 mm longae, 0.9–1.2 mm crassae; stylus crassus 6–8 mm longus stigmate ca. 1 mm longo, ca. 1 mm crasso. Bacca subglobosa, 10–12 mm longa, in maturitate ca. 10 mm crassa, rosea ad atrorubra, seminibus multis 0.9–1.2 mm longis, 0.5–0.7 mm crassis, in ambitu oblongibus vel subtriangularibus. Numerus gameticus chromosomatum, $n = 11$.

Scandent subshrub 0.5–1.5(–2) m tall, glabrous throughout. Branchlets 1–5 dm long, 1–3 mm thick, quadrangular; older branches terete, with pale tan, finely fissured bark. Leaves opposite, subcoriaceous, elliptic to lance-elliptic, acute at base, acute to acuminate at apex, (3–)5–11.5 cm long, (1–)2.5–5 cm wide, dark green above, flushed purple beneath; secondary veins 10–12 on either side of the midvein, margin subentire to denticulate with small, glandular teeth; petiole stout, 1–2 mm thick, red, 4–9 mm long; stipules semisucculent, deltoid, dark when dry, 0.8–1.0 mm long and wide, often connate, deciduous. Flowers numerous in terminal racemes, rarely axillary, or occasionally in 2–3-branched panicles; rachis 5–20 cm long; pedicels erect to spreading, slender, 6–12 mm long, elongating up to 18 mm long in fruit; ovary cylindrical-fusiform, 4–6 mm long, ca. 3 mm thick, lustrous red-pink; floral tube obconic to subcylindric, 2.5–4.5 mm long, 1.5–2.5 mm wide at base, widening to 2.5–4.5 mm wide at rim; sepals broadly lanceolate, 4–6 mm long, 2.5–3.5 mm wide, apex acute, spreading; tube and sepals red to rose-red; petals rose-pink, suborbicular to ovate, 4–6 mm long, 3–4 mm wide, rounded at the base, rounded to acute at the apex; nectary an irregularly to 4-lobed ring-shaped disc adnate to the base of the floral tube, 1–1.5 mm high; filaments dull red, the antisepalous filaments erect and exserted above the rim of the tube, 1–1.5 mm long, the antipetalous filaments reflexed and included in the tube, 0.8–1.4 mm long; anthers white, 1.5–2.0 mm long, 0.9–1.2 mm thick; style

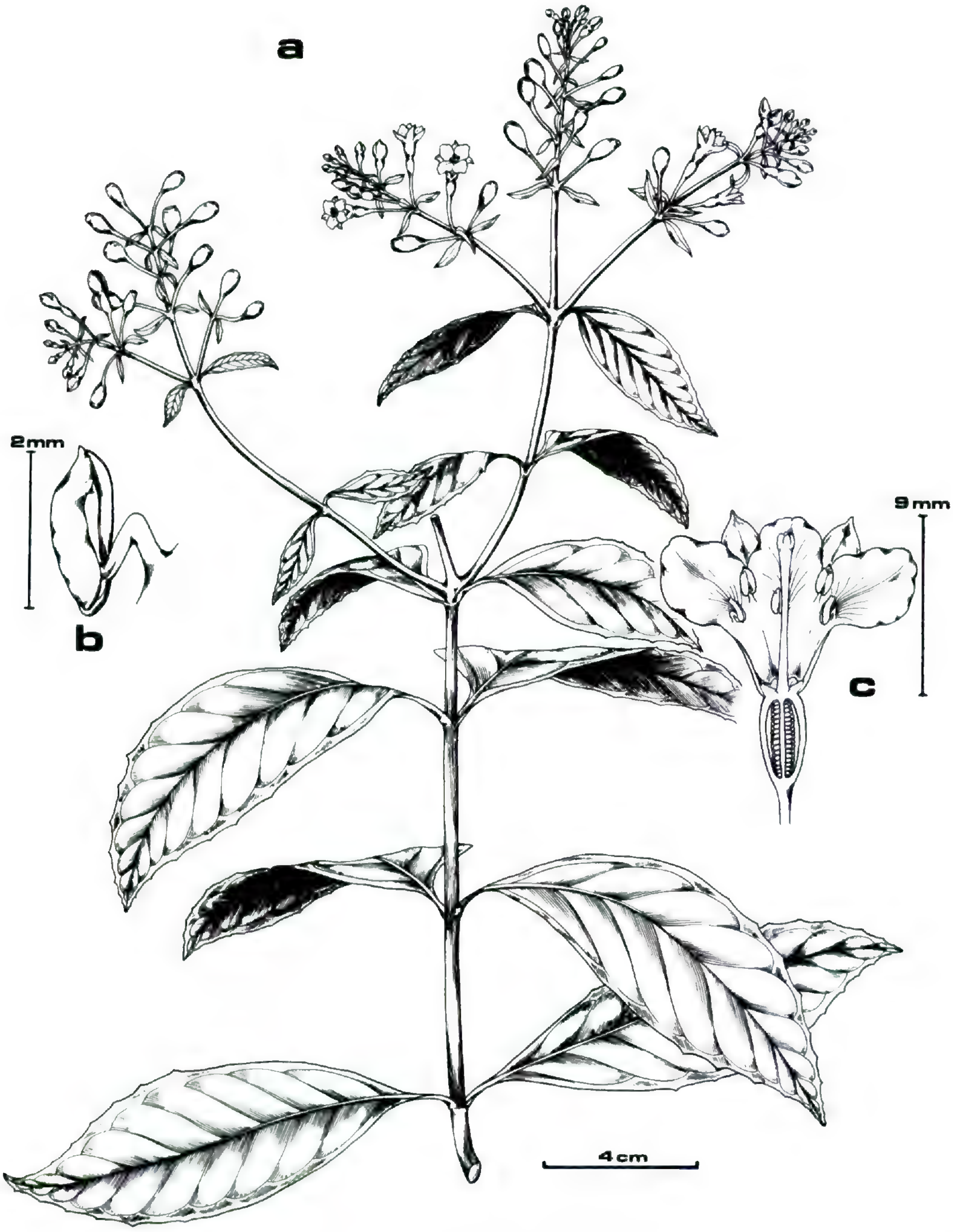


FIGURE 4. *Fuchsia jimenezii* Breedlove, Berry & Raven.—a. Habit; rachis and flowers are divergent to pendant in life.—b. Antipetalous anther.—c. Flower, longitudinal section. From *Wilbur 14238* (MO), Monteverde, Puntarenas, Costa Rica.

stout, 6–8 mm long, the stigma capitate and obscurely 4-cleft at the apex, 1–1.5 mm long, ca. 1 mm thick. Berry subglobose, 10–12 mm long, ca. 10 mm thick when ripe, light to dark red, lustrous; seeds reddish, 0.9–1.2 mm long, 0.5–0.7 mm thick. Gametic chromosome number, $n = 11$.

Distribution: Panama and Costa Rica. Scattered in mostly secondary vegetation of wet evergreen cloud forests from Chiriquí Province of northern Panama

to the northernmost extension of Puntarenas Province of Costa Rica, 1,500–1,900 m (Fig. 2). Flowering throughout the year.

Specimens examined: COSTA RICA, CARTAGO: Ca. 10 km S of Tapantí on road above Río Grande de Orosi, *Burger & Burger 7561* (MO); Tapantí Reserve, Río Dos Amigos, *Croat 36223* (MO); 8.5 km S of Tapantí, *Lent 1372* (BM, F, MO). HEREDIA: Río Vueltas, E slope of Volcán Barba, *Burger & Liesner 6438* (F, GH); Vara Blanca, *Chrysler 5016* (F); Alto de los Robles, San Rafael, *Jiménez 2533* (F); Río Patria, SE slopes of Volcán Barba, *Jiménez 2300* (F); vicinity of Cerro Chompipe between Río la Vueltas and Quebrada Cabrú, *Luteyn & Wilbur 4441* (CAS, DUKE); San Isidro, Cerro de las Lajas, *Standley & Valerio 51567* (US); 12 km NE of San Rafael, *Wilbur et al. 15981* (DUKE); vicinity of Cerro Chompipe, between Río Las Vueltas and Río Nuevo, *Wilbur & Luteyn 18566* (DUKE, MICH, MO). PUNTARENAS: Monteverde, Sierra de Tilarán, *Almeda et al. 2022* (DUKE, MO), *Burger & Baker 9746* (U), *Burger & Gentry 8759* (F), *Haber 434* (MO), *Lorence & Pierce 1722A* (MO), *Palmer 55* (CR), *75* (CR), *171* (CR), *Solomon 5370* (MO), *Wilbur 14238* (DUKE, MO). SAN JOSÉ Vicinity of Cascajal, 3–6 km beyond Las Ñubes, *Almeda et al. 2360* (MO); Alto La Palma, above Río Hondura, *Lent 1341* (DUKE, F, S); near Quebrada Grande, 3 km NW of Cascajal, *Lent 2310* (F); La Hondura, *Standley 36587* (US). PANAMA, BOCAS DEL TORO: Róbalo trail, N slopes of Cerro Horqueta, *Allen 4965* (G, MO, RSA): E slope of La Zorra to Divide, *Kirkbride 831* (MO). CHIRIQUÍ: Bajo Mono-Róbalo trail, W slopes of Cerro Horqueta, *Allen 4816* (G, RSA); trail from Rio Palo Alto road, near peak of Pate Macho, *Hammel 5785* (MO); Cerro Colorado, ca. 32 km from Rio San Felix, *Sullivan 310* (MO), *317* (MO); near Bajo Chorro, *Woodson & Schery 700* (MO).

This species is remarkable in being totally glabrous. The antipetalous stamens reflexed down into the floral tube is found elsewhere in the genus only in sect. *Encliandra,* which differs strongly in its subdioecious to dioecious, axillary flowers, strongly four-lobed stigmas, and few-seeded berries. A gametic chromosome number of $n = 11$ was obtained from *Haber 434*.

Fuchsia sect. **Schufia** (Spach) Munz, Proc. Calif. Acad. Sci. IV. 25:84. 1943.

Schufia Spach, Hist. Nat. Vég. Phan. 4:411. 1835. TYPE: *Fuchsia arborescens* Sims.

Hermaphroditic, morphologically gynodioecious, or subdioecious. Small trees. Leaves opposite or 3–4 verticillate, elliptic to oblanceolate. Flowers numerous and erect in terminal, di- or trichotomously branched panicles, 10–25 cm long and 9–20 cm wide. Floral tube, sepals, and petals nearly equal in length. Nectary annular, smooth to ±4-lobed, adnate to the base of the floral tube. Stamens biseriate, erect, the antisepalous stamens longer than the antipetalous stamens. Berry subglobose, with a waxy bloom when ripe; seeds ca. 50–ca. 100, laterally compressed, oval to irregularly triangular in outline, 1–1.5 mm long, 0.5–0.9 mm wide. Gametic chromosome number, $n = 11$.

Fuchsia arborescens and *F. paniculata* have generally not been separated in the past. *Fuchsia arborescens* was first collected in Mexico in 1790 by Sessé and Mociño, but the name *Fuchsia arborea* Sessé & Mociño was not published until their manuscripts were rediscovered and published in 1888 (McVaugh, 1977). Sims (1825) first published a description and illustration of *F. arborescens*; his plate was dated December, 1825, preceding by just a month Lindley's publication of the same name (Lindley, 1826). Lemaire (1848) recognized that Central American plants of this group had more ridged and serrate leaves than the typical *F. arborescens* from Mexico, and he consequently described his Guatemalan plants as a variety of that species. Subsequently, Lindley (1856) gave specific status to these serrate-leaved plants under the name *F. paniculata*.

The male sterility and floral dimorphism prevalent in most populations of

Fuchsia paniculata have provided another source of confusion in this group. Donnell Smith (1898) first recognized two distinct flower sizes in his Guatemalan collections and called the larger-flowered ones *F. arborescens* var. (?) *megalantha* (perfect-flowered plants). In their field studies of the Panamanian flora, Woodson & Seibert (1937) realized that the different flower sizes were due to sexual differences and termed the species "polygamodioecious." Seibert noted that only the pistillate plants bore fruit and had smaller flowers but larger stigmas than "those plants which are apparently incapable of fructification" (Woodson & Seibert, 1937, p. 196). In his 1943 monograph of the genus, Munz failed to recognize the different sexual morphs and instead named three different forms of *F. arborescens*.

As understood here, *Fuchsia arborescens* consists entirely of hermaphroditic plants and is quite uniform throughout its range. The leaves are larger than those of *F. paniculata* and have a smooth surface and entire margins. The flowers of *F. arborescens* are broader in bud than those of either floral morph of *F. paniculata*, and the anthers are oblong and larger than the ovoid-reniform anthers in perfect flowers of *F. paniculata* (Fig. 5). Also, the stigma of *F. arborescens* is always conspicuously four-lobed and well exserted above the anthers.

Fuchsia arborescens and *F. paniculata* are allopatric except for a small overlap of ranges in northern Oaxaca and in Veracruz. Some unusually pubescent collections occur in the area of overlap in Oaxaca. In *F. paniculata*, *Jurgensen 530* (G) and *Galeotti 3035* (W) are pilose, and short, dense pubescence is found on two collections referable to *F. arborescens*, *Smith 615* (GH) and *Karwinsky? 46* (G). This last specimen has large leaves with serrulate margins, but the flowers and stamens agree much more with those of *F. arborescens* than with those of *F. paniculata*.

The general appearance of these fuchsias strongly suggests that of certain Rubiaceae. In northern Panama, *F. paniculata* is sympatric with *Psychotria angustifolia* HBK, and the two can only be distinguished upon close examination. They probably share common pollinators.

5. Fuchsia arborescens Sims, Bot. Mag. *pl. 2620,* 1825. Lindl., Bot. Reg. *pl. 943.* 1826.—TYPE: *Plate 2620* in Sims, Bot. Mag. 1825, lectotype, here designated, from cultivated material grown from seed sent in 1823 by George Bullock, who obtained the seeds from plants in cultivation at the Botanic Garden in Mexico City. The Mexican plants were probably sown by Martín Sessé and are likely progeny of the type specimen of *Fuchsia arborea* Sessé & Mociño. *Schufia arborescens* (Sims) Spach, Hist. Nat. Vég. Phan. 4:411. 1835. *Fuchsia arborescens* var. *typica* Munz, Proc. Calif. Acad. Sci. IV. 25: 85, *pl. 14, fig. 75.* 1943. FIG. 5a.

Fuchsia arborea Sessé & Mociño, Pl. Nov. Hisp. 58. 1888. TYPE: Uruapán, Michoacán, Mexico, Sept. 1790, *Martín Sessé, José Mociño, Juan Diego del Castillo & José Maldonado 5216* (F 845520, lectotype here designated; MA, possible isolectotype; the one specimen of *F. arborescens* at MA has a Ruiz & Pavón label and is annotated as *F. paniculata*, but it is most probably mislabelled from a Sessé et al. collection. The sheets at MA and F appear to have been taken from the same plant).

Hermaphroditic. Erect, woody shrubs or small trees 3–8 m tall, mostly glabrous throughout. Branchlets ascending, 1–4 dm long, 2–5 mm thick, subtriangular to

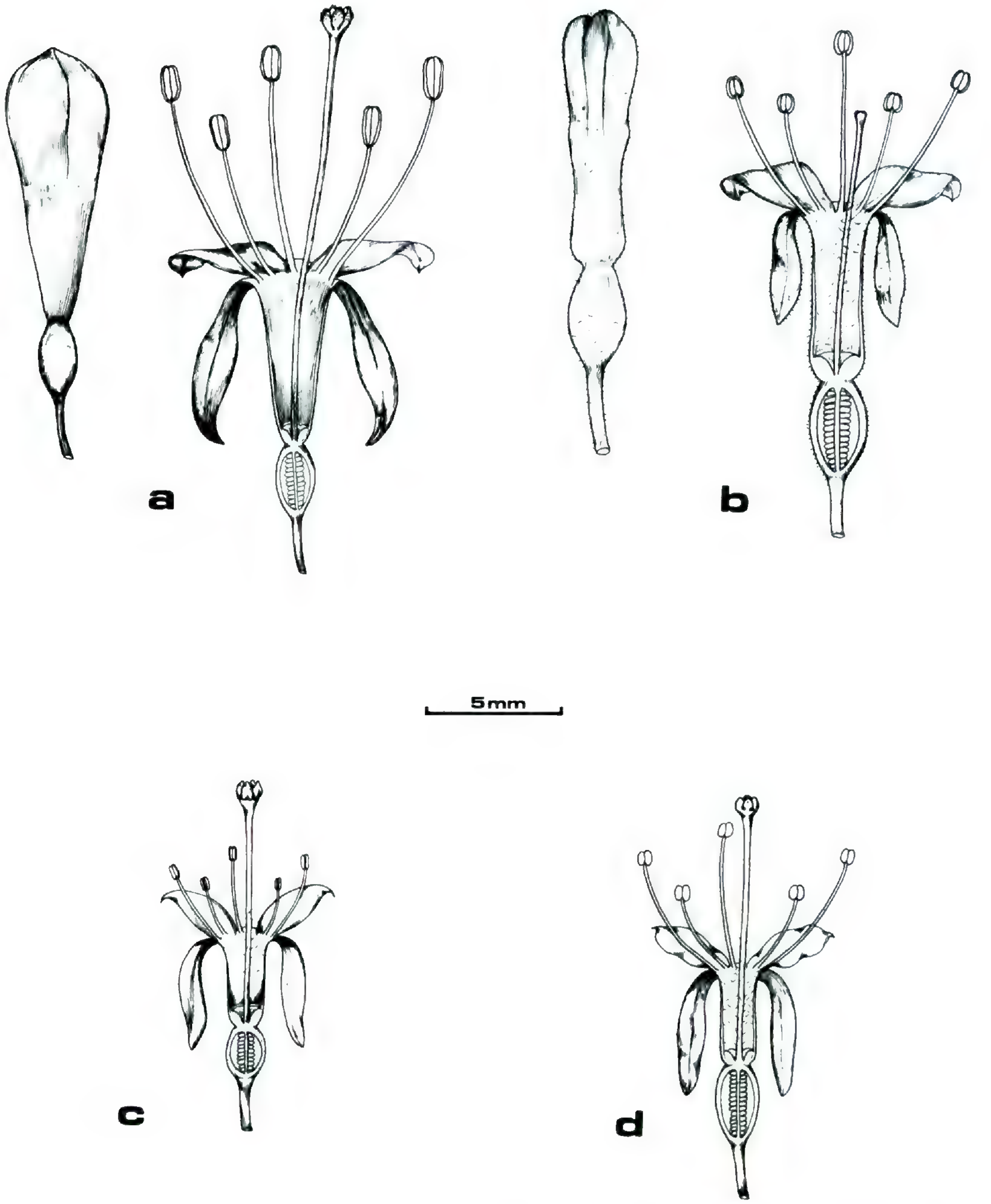


FIGURE 5. a. *Fuchsia arborescens* Sims. Bud and flower, longitudinal section. From *Feddema 2872* (MO), Guerrero, Mexico. b–d. *Fuchsia paniculata* Lindley.—b. Bud and perfect flower, longitudinal section; from a gynodioecious population. From *Breedlove 42742* (MO), Chiapas, Mexico.—c. Pistillate flower, longitudinal section. From *Raven 20969* (DS), Cartago, Costa Rica.—d. Perfect flower, longitudinal section, from a hermaphroditic population. From *Ventura 3631* (MO), Veracruz, Mexico.

quadrangular; older branches and main trunk 5–25 cm thick. Leaves opposite or 3–4-verticillate, firmly membranous to subcoriaceous, smooth, elliptic to oblanceolate or obovate, acute to narrowly cuneate at base, acute to acuminate at apex, 10–21 cm long, 4–8 cm wide, deep lustrous green above, paler below; margin entire; petiole 12–30 mm long; stipules broadly triangular, occasionally connate, 0.8–1.2 mm long, 1.0–1.5 mm wide, deciduous. Flowers erect and nu-

merous in terminal, di- to trichotomously branched panicles, 10–25 cm long, 9–20 cm wide; pedicels erect, slender, 9–18 mm long; floral tube subcylindric to obconic, 3.5–6 mm long, 1–1.5 mm wide at base, ± enlarged around nectary, 2–4 mm wide at rim, usually glabrous inside and outside; flowers widened toward apex in bud; sepals oblong to lanceolate, acuminate, 4–11 mm long, 1.5–2.5 mm wide, spreading to reflexed at anthesis; tube and sepals rose-purple; petals lavender, lance-oblong to elliptic, 4–9 mm long, 1.5–3 mm wide, broadly acute at base, acute at apex, erect to spreading; nectary a smooth and irregularly lobed ring 1–1.6 mm high adnate to the base of the tube; antisepalous filaments 5–12 mm long, antipetalous ones 3–9 mm long, pink-purple; anthers oblong, 1.5–2.3 mm long, 1–1.5 mm thick; style 9–17 mm long, glabrous, pink, the stigma always exserted above the anthers, 1.5–3 mm wide, with 4 blunt lobes 1–2 mm long, lavender. Berry subglobose, 8–12 mm long, 7–10 mm thick, purple with a glaucous, waxy bloom when ripe; seeds 1–1.5 mm long, 0.5–0.8 mm thick. Gametic chromosome number, $n = 11$.

Distribution: Mexico. Occasional small trees mostly in barranca vegetation (moist ravines) of pine-oak forest in the Sierra Madre Occidental from Durango to Oaxaca and through the Trans-Mexican Volcanic Belt to Veracruz and then into northern Oaxaca, 1,750–2,500 m (Fig. 6). Flowering mostly in the dry season (December–May), but also well into the wet season.

Representative specimens examined: MEXICO, DURANGO: El Palmito, *Breedlove & Gregory 14250* (DS); ca. 8 km NE of Palmito, *Gentry & Gilly 10629* (MICH). GUERRERO: Filo del Caballo, *Breedlove 15832* (DS); Cruz de Ocote, 50–60 km W of Chilpancingo, *Feddema 2872* (DUKE, MICH, MO, PH); Campo Morado, Mina, *Hinton et al. 11173* (GH); Galeana, Toro Muerto, *Hinton 14213* (DS, F, GH, NA, NY, US); W of Cerro Azul, Mina, *Hinton et al. 14952* (GH); Milpillas-Ayotac road, ca. 24 km SW of Filo de Caballo, *Reveal et al. 4266* (MO); San Antonio-Buenos Aires, Montes de Oca, *Hinton et al. 14013* (GH, MICH, NA, NY, U); W of Petlacala, Mina, *Mexia 9052* (BH, G, GH, LL, MO, NY, S, U, UC); Omiltemi, W of Chilpancingo, *Rzedowski 15992* (MICH). JALISCO: W slopes of Sierra de San Sebastián, 15–30 km N of Mascota, *Anderson & Anderson 5659* (DUKE, MICH); ca. 24 km SW of Chante, Sierra Manantlán, *Gentry & Gentry 23514* (MICH); Sierra de Halo, *McVaugh & Koelz 1236* (MICH); 15 km SE of Autlán, trail from Chante to Rancho Manantlán, *McVaugh 10267* (DUKE, G, MICH, MO, TEX); Nevado de Colima, near Atenquique, *McVaugh et al. 11770* (MICH, RSA). MÉXICO: Tequexquipan, *Hinton 3520* (GH, MICH, NY, US); Rincón, Temascaltepec, *Hinton et al. 5287* (GH, NY, US); Cumbre of Cimientos, Temascaltepec, *Hinton et al. 8850* (GH); Cerro de Corona, Zacualpán, *Matuda 30739* (MEXU). MICHOACÁN: Coalcomán, Barroloso, *Hinton 15756* (DS, MICH, NY); ca. 28 km E of Morelia, *King & Soderstrom 5020* (MICH, NY, TEX, UC, US); Falls of Tzararacua, S of Uruapan, *Langman 3289* (NA, PH); Uruapan, *Leavenworth & Hoogstraal 1257* (F); Sierra de Manantlán, *McVaugh 13921* (MICH). MORELOS: Sierra de Morelos, *Hinton et al. 17096* (MICH): Tepoxtlán, *Miranda 517* (MEXU); Tlayacapan, *Paray 2109* (MEXU); mountains above Cuernavaca, *Pringle 6825* (BH, BM, BR, F, G, GH, K, LE, M, MICH, MO, NY, PH, POM, RSA, S, UC, VT, W, Z). OAXACA: Finca La Soledad, 184 km S of Oaxaca, *Alexander 587* (MEXU, MICH, NY, UC, US); near San Juan, *Arnold 3* (CAS); Coyula, Cuicatlán, *Cancino 2438* (US); Highway 175, 6 km S of Suchixtepic, *Croat 46026* (MO); Hacinda de San Luis, *González 426* (GH); Cañada de los Molinos, valley of Oaxaca, *Jurgensen 489* (BM, G); La Cumbre de los Molinos, *Karwinski? 46* (G); between Juquila and Nopala, *Nelson 2417* (US); Sierra de San Felipe, *Pringle 6242* (A, BH, BM, BR, F, G, GH, LE, M, MO, NY, PH, POM, RSA, S, UC, US, VT, W, Z); 4 km S of Lachao, Oaxaca-Puerto Escondido, *Rzedowski 19541* (MO). PUEBLA: San Vicente, near Puebla, *Nicolas in 1909* (G). VERACRUZ: Jalapa, *Galeotti 3035* (BR, LE, NY); La Luz, near Córdoba, *Kerber s.n.* (G); El Esquilón, municipio Jilotepec, *Ventura 4843* (MICH, MO).

Cultivated specimens: FRANCE: 1826 (G). GREAT BRITAIN: 1826, *Lindley 943* (CGE); Edinburgh, 1964, *Meyer 8211* (NA). INDIA: Madras, 1850, *Golley 389* (LE). MADEIRA: Santa Roque, *Hilldebrand s.n.* (Z). MEXICO, VERACRUZ: Orizaba, 1885, *Gray s.n.* (GH). NETHERLANDS: Baarn, 1955, *Mennaga 4137* (BH, U). WEST GERMANY: Berlin, 1963, *R181* (B).

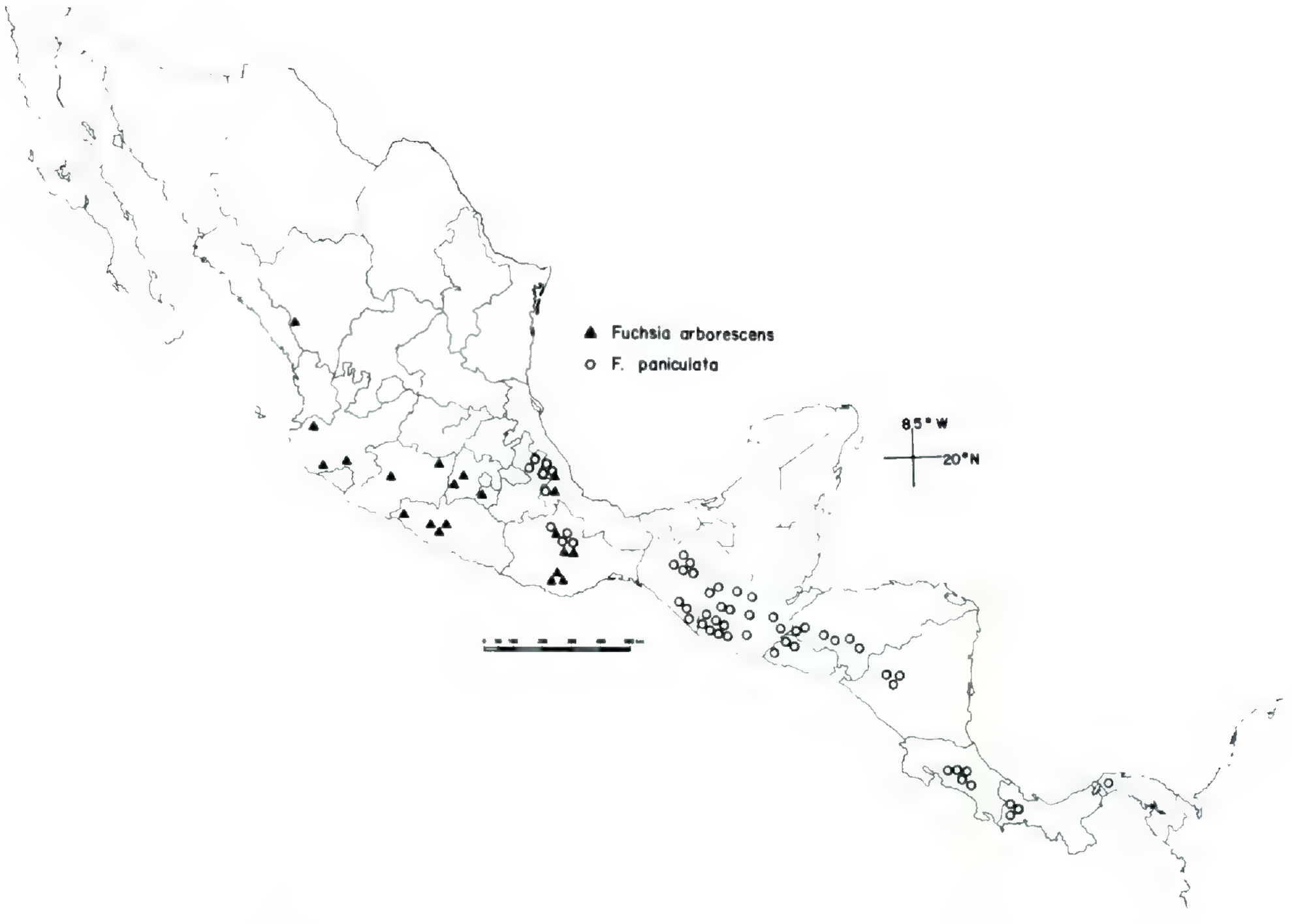


FIGURE 6. Distribution of *Fuchsia arborescens* and *F. paniculata* (sect. *Schufia*).

Fuchsia arborescens is commonly found in barrancas, or deep moist ravines, mostly in the Sierra Madre Occidental of Mexico. In "La Vegetación de Nueva Galicia," Rzedowski & McVaugh (1966) list *F. arborescens* as one of the low tree components of the "mesophytic mountain forest" formation, which occurs very discontinuously throughout the Sierra Madre and occupies less than 1% of the total vegetation cover for the area. This is the most moist formation of central, western Mexico, with rainfall estimated at 1,000–2,000 mm per year; the formation is essentially restricted to the barrancas, where a higher humidity can be maintained than in adjacent oak-pine forest. *Fuchsia fulgens* and *F. decidua* are listed as epiphytes in the same formation.

A diploid gametic chromosome count of $n = 11$ was obtained from *Breedlove 18713*. A somatic count of $2n = 22$ was obtained by D. Breedlove from a cultivated plant at Stanford University, California, grown from seeds collected at the University of Mexico Botanic Garden in Mexico City (no voucher). An additional diploid somatic count is cited by Kurabayashi et al. (1962) for *Raven 14745* (RSA).

6. Fuchsia paniculata Lindley, Gard. Chron. 1856:301. 1856. TYPE: Guatemala, 1855, *George U. Skinner 48* (CGE lectotype, here designated; photograph, MO).—FIGS. 5b, c, d.

Fuchsia arborescens auct. non Sims, 1825: Essig, Nat. Hort. Mag. 13:2, *photo*, 3. 1934; Munz in

Woodson & Schery, Ann. Missouri Bot. Gard. 45:218. 1959; Standl. & Williams, Fieldiana, Bot. 24(7):528. 1963.

Fuchsia arborescens var. *syringaeflora* Lemaire, Fl. Serres Jard. Eur. 4:416, *fig.* 1848. TYPE: Cultivated in the garden of L. van Houtte, France, from seeds received in 1847 from Guatemala (K lectotype here designated); Sieb. & Voss. in Vilm., Blemengart, ed. 3, 1:332, *t. 84. fig. 335.* 1896. *Fuchsia syringaeflora* (Lem.) Carrière, Rev. Hort. 45:311, *fig.* 1873.

Fuchsia arborescens var. (?) *megalantha* Donnell Smith, Bot. Gaz. 18:2. 1893. TYPE: Volcán Acatenango, Dept. Sacatapéquez, Guatemala, Mar. 1892, *John Donnell Smith 4269* (US, holotype; GH, K, isotypes).

Fuchsia leibmannii H. Léveillé, Bull. Geogr. Bot. 22:24. 1912. TYPE: Volcan Irazú, ca. 2,800 m, Prov. San José, Costa Rica, 1845–1848, *A.S. Oersted 3297* (C, holotype; photograph, GH; G, isotype). Oersted, who collected in Costa Rica and Nicaragua from 1845 to 1848, and F. Liebmann, who collected in Mexico from 1840 to 1842, collaborated jointly on their collections upon their return to Europe. Léveillé mistook the type for a Liebmann collection, hence the specific epithet and the locality cited in the protologue as "Mexique: mont Frasu" (= Irazú).

Fuchsia arborescens forma *tenuis* Munz, Proc. Calif. Acad. Sci. IV. 25:86. 1943. TYPE: Vara Blanca de Sarapiquí, between Volcán Poás and Volcán Barba, 1,740 m, Prov. Heredia, Costa Rica, Oct., 1937, *Alexander Skutch 3357* (US, holotype; A, MO, NY, S, isotypes).

Fuchsia arborescens forma *parva* Munz, Proc. Calif. Acad. Sci. IV. 25:86. 1943. TYPE: Finca Pirineos, below Santa María de Jesús, Dept. Quezaltenango, Guatemala, *Paul Standley 68287* (POM, holotype; F, isotype).

Gynodioecious or subdioecious. Erect woody shrubs or small trees 3–8 m tall, usually glabrous. Branchlets ascending, 1–4 dm long, 2–5 m thick, subtriangular to quadrangular; older branches and main trunk 2–15 cm thick. Leaves opposite or 3–4-verticillate, subcoriaceous, elliptic to oblanceolate, acute to narrowly cuneate at base, acute to acuminate at apex, 5–15.5 cm long, 2–5.5 cm wide, deep lustrous green above, paler below; margin minutely to coarsely serrate; petiole 8–26 mm long; stipules triangular, often connate, 0.8–1.2 mm long, 0.7–1.5 mm wide, deciduous. Flowers erect and numerous in terminal, di- to trichotomously branched panicles, 10–14 cm long, 9–12 cm wide, narrowed towards the apex. *Perfect flowers:* Pedicels slender, 8–12 mm long; floral tube cylindric to subobconic, 4–8 mm long, 1–2 mm wide at base, 1.5–3 mm wide at the rim, often pilose within; sepals lanceolate, 5–10 mm long, 1.1–2.5 mm wide, spreading to reflexed at anthesis; tube and sepals rose-purple; petals lavender, lanceolate to elliptic, 4–10 mm long, 1.1–3.5 mm wide, acute at both ends, erect to spreading; nectary smooth to irregularly lobed ring 1.3–2 mm high adnate to the base of the tube; antisepalous filaments 4–13 mm long, antipetalous ones 2–11 mm long, pink; anthers broadly ovoid to reniform, 0.8–1.6(–2) mm long, 0.7–1.4 mm thick: style sparsely pilose, either exserted beyond anthers with a shortly 4-lobed stigma or included below the anthers and the stigma strongly reduced, lavender. *Pistillate flowers:* Similar to the perfect ones except in the following characters: floral tube smaller, 3–5.5 mm long, 0.7–1.7 mm wide at base, 1.5–2.2 mm wide at rim; sepals 3.5–7 mm long, 0.7–1.3 mm wide; petals 2.3–4.5 mm long, 0.6–1.3 mm wide; nectary 0.8–1.4 mm high; antisepalous filaments 1.5–4.9 mm long, antipetalous ones 1.0–3.9 mm long; anthers abortive, 0.4–0.8 mm long, 0.2–0.6 mm thick; style stout, 7–11 mm long, the stigma well exserted above the stamens, 4-lobed, lobes 0.6–1.9 mm long. Berry subglobose, 4–9 mm long, 4–7 mm thick, purple with a glaucous, waxy bloom; seeds 1–1.4 mm long, 0.5–0.8 mm thick. Gametic chromosome number, $n = 11$.

Distribution: Mexico to Panama. Frequent in moist oak-pine and evergreen

cloud forest from Veracruz, Mexico south to central Panama. North of the Isthmus of Tehuantepec, it occurs only on the wet Caribbean facing-slopes in Puebla, Veracruz, and Oaxaca. This species grows at elevations of (800–)1,200–3,000 m (Fig. 6). Flowering throughout the year.

Representative specimens examined: MEXICO, CHIAPAS: Zinacantán, NW of Navenchauc, *Breedlove 5971* (DS); Chamula, *Breedlove 7145* (DS); Rayón, N of Pueblo Nuevo, near Puerto el Viento, *Breedlove 10172* (DS, BM); Huistán, *Breedlove 7343* (BM); N & W slopes of Cerro Mozotal, road Huixtla-El Porvenir, *Breedlove & Smith 22793* (MO); Cerro Huitepec, W of San Cristóbal las Casas, *Breedlove 23007* (MO); 16 km NW of Rizo de Oro, SE of Cerro Baúl, *Breedlove 24891* (MO); SE slopes of Volcán Tacaná, above Talquián, *Breedlove 29475* (MO); near summit of Chuchil Ton, NE of Bochil, *Breedlove 34657* (MO); Laguna Pojo, near Lago Tsiskla, *Breedlove 37087* (MO); logging road, Las Margaritas-Campo Alegre, *Breedlove 41114* (MO); near Niquivil, junction of ridge to Cerro Boquerón, *Breedlove 42742* (MO); 4 km N of Colonia San José, ca. 12 km S of Layón, *Hansen et al. 1688* (MICH); San Bartolo, *Linden 39* (G); Mt. Ovando, *Matuda 437* (F, MEXU, MICH, US); Siltepec, *Matuda 812* (MEXU, MICH); Mt. Pasitar, *Matuda 1695* (A, MEXU, MICH, NY); Volcán Tacaná west, *Matuda 2924* (A, LL, IPN, MICH); Mt. Pale, near Porvenir, *Matuda 4670* (A); near Motozintla, *Matuda 15447* (LL, MEXU, TEX); Cerro del Boquerón, *Purpus 6970* (GH, MO, NY, UC, US); near Pueblo Nuevo Solistahuacán, *Raven & Breedlove 20004* (DS, GH); Jitotal, *Roe et al. 1182* (MICH). OAXACA: Cuyamecalco, Cuicatlán, *Conzatti 3497* (MEXU); ca. 60 km N of Ixtlán de Juárez, road to Tuxtepec, *Denton 1688* (MICH); Tonaguía, *Galeotti 3035* (LE, W); Nolasco, *Galeotti 3058K* (F); Rt. 175 near Cerro Pelón, 34 km SW of Valle Nacional, *Hill 1730* (MO); Monte Tepitongo, Sierra San Pedro Nolasco, Talea, *Jurgensen 530* (G); Vista Hermosa to Comaltepec, *Martínez 242* (MO); ca. km 125 of Tuxtepec-Oaxaca road, *Smith & Tejeda 4497* (NA); ca. 16 km S of Villa Hermosa, *Torke et al. 504* (MO). PUEBLA: Road to Presa de Apulo, N of Oriental-Tezuitlán road, *Koch & Fryxell 7716* (MO); NE of Tezuitlán, *Pineda 686* (MICH); San Juan Abuacatlán, *Salazar s.n.* (MEXU); Colihuit, municipio Hueytamalco, *Ventura 389* (MICH); Agua de Obispo, municipio Tezuitlán, *Ventura 13641* (MO); ca. 8 km NE of Teziutlán, road to Tlapacoyán, *Webster & Breckon 15463* (DUKE, GH). VERACRUZ: Orizaba, *Botteri 58* (F, GH); Jalapa, *Galeotti 3035* (G); Cerro de San Cristobal, W of Orizaba, *Langman 3587* (PH); Mirador, *Liebmann 3237* (BH, BR, G, GH, MO, MSC, UC, US); Huahesco, *Mohr 1865* (US); Zacuapan, Tenampa, *Purpus 4330* (A, BM, GH, MO, UC); Chiconquiaco, cañada del Huérfano, *Rosas 580* (MO); Ahuacatitlán, municipio Jalacingo, *Ventura 283* (MICH, MO); Lomas de Santa Rita, municipio Yecualta, *Ventura 3631* (MO); Xico, *Ventura 4519* (MICH); Tepezingo, *Ventura 15051* (MO); Cuesta Grande de Jalacingo, *Schiede & Deppe 526* (LE, W). GUATEMALA, ALTA VERAPAZ: Chucaneb, *Donnell Smith 182* (G, GH, PH); Tactic, *von Tuerckheim 8395* (A, F, M, NY, US); Cobán, *von Tuerckheim 11713* (BR, C, F, FI, G, GH, LE, MO, US, W, Z). BAJA VERAPAZ: Unión Barrios, *Contreras 11245* (MO); ca. 7 km NE of Purulhá, *Croat 41329* (MO). CHIMALTENANGO: Tres Cruces, N side of Volcán Acatenango, *Beaman 3996* (GH); Volcán Acatenango, *Hunnewell 14764* (GH); Chichavac, *Skutch 255* (US); Las Calderas, Volcán Acatenango, *Standley 61962* (F); Patzum, *Williams & Molina 11843* (F, GH): road to Panajachel, between Los Idolos and Chochoyos, *Williams 16214* (F). CHIQUIMULA: Concepción de las Minas, Montaña Norte, *Steyermark 31042* (F). ESCUINTLA: S slopes of Volcán de Agua, *Almeda 756* (DUKE). GUATEMALA: 6 km SE of Guatemala City, *Harmon 1980* (MO); below San Lucas and Guatemala City, *Molina et al. 16662* (F). HUEHUETENANGO: Sierra de los Cuchumatanes, San Mateo Ixtatán, *Breedlove 11636* (DS); Jacaltenango, *Seler & Seler 2599* (GH); Yalambo, *Seler & Seler 2869* (GH, US). QUEZALTENANGO: road to Fuentes Georginas, *Boeke 164* (MO); 3 km S of Santa María Electric Plant, *Roe et al. 718* (G); Volcán Zunil, *Skutch 877* (A); above Mujulía, *Standley 85487* (F); Montaña Chicharro, lower SE slopes of Volcán Santa María, *Steyermark 34282* (A, F). QUICHÉ: Nebaj, *Contreras 5083* (LL); San Miguel Uspantán, *Heyde & Lux 3001* (G, GH, M, MO, NY, POM, US); RETALHULEU: Finca Helvetias, *Muenscher 12430* (BH). SACATEPÉQUEZ: Volcán Acatenango, *Donnell Smith 2469* (GH, US); Volcán de Fuego, *Salvin s.n.* (W); Santa María de Jesús, Volcán de Agua, *Standley 65006* (F). SAN MARCOS: La Trinidad, above San Rafael, *Croat 40881* (MO); 22 km W of San Marcos, *Harmon & Fuentes 4744* (MO); Volcán Tacaná, San Rafael, *Steyermark 36331* (F, POM); Finca El Porvenir, *White 5421* (MO); ca. 15 km W of San Marcos slopes of Cerro Tumbador, *Williams et al. 23061* (F, G); near Alta Fraternidad, between San Rafael Pie de la Cuesta and Palo Gordo, *Williams et al. 27163* (F). SOLALÁ: 2 km W of Godinez, *Harmon & Dwyer 2624* (GH, MO); above Lake Atitlán, W of Panajachel, *Williams et al. 25347* (F). SUCHITEPÉQUEZ: S slope of Volcán Atitlán, *Hatch & Wilson 361* (BH, F); Finca Mocá, *Skutch 1552* (A, F). ZACAPÁ Sierra de las Minas, Finca Planados, *Steyermark 29996* (F); Volcán de Monos, *Steyermark 42382* (BH, F). EL SALVADOR, CHALATENANGO: E slopes of Los Esemiles, *Tucker 1006* (BG, G, LL, MICH, NY, P, PH, UC, US). SANTA ANA: Volcán Santa Ana, *Carlson 698* (A, F, MO, UC); Cerro Miramundo, *Carlson 987* (F); Cerro Montecristo, 24 km NE of Metapán, *Croat 42341* (MO). HONDURAS, CORTÉS: Montaña San Idalfonso, *Molina 11462* (F). EL PARAÍSO: Mon-

taña de Yuscarán, *Rodríguez 1956* (F); El Volcán, *Williams & Molina 12187* (F, GH, MICH, MO). FRANCISCO MORAZÁN: Mt. Uyuca, near Zamorano, *Carlson 2459* (GH); 6 km N of Tegucigalpa, *Clewell 3016* (MO); Mt. San Juancito, *Williams & Molina 12752* (F, GH); Montaña La Tigra, ca. 15 km NW of Tegucigalpa, *Williams et al. 23266* (BM, F, G, GH, LL, MICH, NY, UC, US, W). INTIBUCA: near La Esperanza, *Hazlett 1244* (MO); Cordillera de Opalaca, Calaveras, *Molina 6434* (US). LA PAZ: Sabanetas, Cordillera Guajiquiro, *Molina & Molina 13918* (F); Montaña Verde, Cordillera Guajiquiro, *Molina 24392* (F). OCOTEPEQUE: 2 km E of Continental Divide on road between Nueva Ocotepeque and Santa Rosa de Copán, *Harmon & Dwyer 4104* (GH, MO); Mt. Cocal, Cordillera Merendón, 20 km W of Ocotepeque, *Molina 2214* (F); El Portillo, Cordillera Merendón, 20 km E of Nueva Ocotepeque, *Molina et al. 31353* (MO). NICARAGUA, JINOTEGA: Cordillera Isabela, Macizos de Peñas Blancas, *Grant 7334* (A, F); Hwy 3, ca. 2 km NW of Aranjuez road, *Stevens 9186* (MO); ca. 8 km S of Jinotega, *Wilbur & Almeda 16510* (DUKE, MO). MATAGALPA: between Jinotega and Matagalpa, *Bunting & Licht 983* (DUKE, F); Santa María de Ostuma, *Williams et al. 23422* (F, G, W); road to La Fundadora, N of Santa María de Ostuma, *Williams et al. 24955* (F, G); near Xelaju, *Williams et al. 29239* (GH). COSTA RICA, ALAJUELA: Highway 120 to Volcán Poás, 1.5–3 km from the crater, *Almeda 382* (DUKE); Palmira del Naranjo, *Brenes 3521* (F, NY); ca. 12 km N of Carrizal, between Volcán Poás and Volcán Barba, *Croat 35464* (MO); Zarcero, Palmira, *Jiménez 2567* (F); Palmira, *Smith 2145* (A, NA); Volcán Poás, *Smith 6504* (GH, POM, US). CARTAGO: 20 km SE of Empalme, *Burger & Stolze 5237* (DUKE, F); near Volcán Irazú, *Carlson 3581* (F, GH, S); Trinidad to Volcán Turrialba, *Lent 722* (MO); Río Tiribí, road from Ipis to Tierra Blanca, *Lellinger & White 993* (F, MICH, MO); Volcán Turrialba, *Pittier 7508* (F, MO, US); 1 km above El Empalme, *Raven 20969* (DS); below San José de Chicua, road to Volcán Irazú, *Raven 20974* (DS); Cerro Guardián, S slope of Irazú, *Webster et al. 12143* (F); ca. 4 km NE of Pacayas towards Santa Cruz de Tenerife, *Wilbur & Luteyn 13890* (F, GH, MO); ca. 4 km E of Rancho Redondo, SW flank of Volcán Irazú, *Wilbur 14273* (DUKE, MO); between Hacienda Central and Finca Quemado, *Wilbur 14339* (DUKE). GUANACASTE: ca. 7 km NE of San Vicente, above Cascajal, *Wilbur & Almeda 16720* (DUKE). HEREDIA: Vara Blanca intersection, trail to Volcán Poás, *Almeda et al. 2198* (DUKE); Porrosatí, N of Barba, *Crosby & Crosby 6611* (MO); Los Cartagos, Volcán Poás road, *Raven 20980* (DS, GH); Vara Blanca de Sarapiquí, *Skutch 3357* (A, G, MO); Volcán Barba Massif, *Tonduz 1734* (W); San Rafael, E of Vara Blanca, *Utley & Utley 4169* (MO); Volcán Barba, *Wilbur & Teeri 13679* (DUKE, F, GH, MICH, MO). SAN JOSÉ: Las Ñubes, *Allen 713* (A, MO); Abra, Chirripó Massif, *Davidse & Pohl 1534* (MO); between Guayabillos and Cabeza de Vaca, *Dodge & Thomas 4936* (GH, MO); Randho Redondo, *Dodge & Thomas s.n.* (MO); Cerro de la Muerte to San Isidro del General, *Lewis 5047* (DUKE); 5 km N of Santa María de Dota, *Lent 3910* (MO); ca. 6 km N of Copey, *Little 6016* (A, MO); El Empalme, *Stork 4545* (MICH, UC); La Palma, *Tonduz 7410* (BM, F, GH, MO, POM, US); Copey, *Tonduz 11666* (G, GH, W); ca. 7 km NE of San Vicente, above Cascajal, *Wilbur & Almeda 16720* (DUKE); above Quebrada Varela, E of San Isidro, *Wilbur & Luteyn 18177* (DUKE). PANAMA, CHIRIQUÍ: Nueva Suiza, *Allen 1351* (GH, MO); Cerro Punta, *Allen 3505* (BM, G, GH, MO, S, U); Finca Arco Iris, Boquete to Palo Alto, *Béliz 210* (MO); 2 km towards Cerro de la Muerte, *Correa 1256* (COL, DUKE, MO); between Alto de Guayabo and continental divide, *Correa et al. 2821* (MO); Monte Rey, above Boquete, *Croat 15772* (MO); above Guadelupe, *Croat & Porter 16021* (MO); La Cumbres, near Cerro Punta, *Croat & Porter 16136* (MO); Cerro Azul, E of Boquete, *Croat 26838* (MO); N of San Félix, near Chiriquí-Bocas del Toro border on road to Cerro Colorado, *Croat 33485* (MO); La Popa, above Boquete, *D'Arcy & D'Arcy 6356* (MO); Alto Respinga, *D'Arcy 9950* (MO); valley of Río Viejo, N of Volcán City, *Duke 8997* (MO); Cerro Horqueta, *Duke et al. 13633* (DUKE, MO); Finca Collins, *Ebinge 689* (MO); Cerro Punta to Las Ñubes, *Hammel 1371* (MO); N slope of Volcán Barú, E of Bajo Chorro, *Hammel 2992* (MO); Cerro Hornito, *Hammel 3052* (MO); Las Ñubes, *Liesner 289* (GH, MO); 8–15 km from Hato de Volcán, *Luteyn 844* (DUKE); Alto Quiel to Bajo Mono, *Luteyn 3708* (DUKE); Bajo Grande to Cerro Punta, *Nee 9973* (GH, MO); upper Río Chiriquí Viejo, vicinity of Monte Lirio, *Seibert 246* (MO); Volcán Barú, near Cerro Punta, *Stern & Chambers 86* (A, MO); El Volcán, *White 4* (GH, MO); Bajo Quiel to Bajo Mono, *Wilbur et al. 11992* (DUKE); S slopes of Cerro Horqueta, N of Boquete, *Wilbur et al. 13443* (DUKE); Casita Alta, Volcán de Chiriquí, *Woodson et al. 797* (A, MO, NY, POM). PANAMÁ: Cerro Jefe, 15–20 km beyond Goofy Lake (Lago Cerro Azul), *Duke 8029* (MO).

Naturalized specimens: COLOMBIA, CUNDINAMARCA: Nemocón, between road and railroad tracks, *Garcia Barriga 19387* (COL, US). BOYACÁ: Labranzagrande, *Guevara 389* (US). SRI LANKA: Nuwara Eliya to Hakgala, just beyond pass to Nuwara Eliya, Rte. A-5, *Read & Desautels 2278* (MO). TANZANIA: Kiefingelo, W of Usumbara, *Greenway 5896* (FHO, K). UNITED STATES, HAWAII: bulldozed Kilauea Forest Reserve, Hawaii, *Degener & Degener 31130* (A, B, NA, Z); ravines over lava, Oahu, *Leith et al. s.n.* (MO).

Cultivated specimens: COLOMBIA, CUNDINAMARCA: Bogotá, *Duque-Jaramillo 2970* (COL, NY). FRANCE: Van Houtte nurseries, 1849 (K). KENYA: Nairobi, 1973, *Raven 26162* (MO). NEW ZEALAND:

Whangarei, originally brought from Tahiti, *Engelhorn s.n.* (MO). ZIMBABWE: Salisbury, *Biegel 4406* (NA). SRI LANKA: Hangola Garden, *Marcovicz in 1927* (LE). UNITED STATES, CALIFORNIA: Santa Barbara, 1970, *Hall 7736* (UC); Berkeley, *Raven 49.801* (DS); Los Angeles, 1901, *Braunton s.n.* (BH). MASSACHUSETTS: Harvard University, Boston, 1876 (GH). HAWAII: "29 Miles," Volcano, Hawaii, *Degener & Degener 31131* (B, MO).

Fuchsia paniculata has leaves with minutely to coarsely serrate margins and a ridged surface; its flowers are consistently more slender and generally smaller than those of *F. arborescens,* but they are much more variable. Apparently all populations of *F. paniculata* north of the Isthmus of Tehuantepec consist entirely of hermaphroditic plants; the flowers are more or less uniform, with small (less than 1 mm long), reniform anthers, and exserted, moderately four-lobed stigmas (Fig. 5d). The populations south of the Isthmus of Tehuantepec, however, are morphologically gynodioecious with perfect flower morphs of different populations varying in style, length, and stigma size. The perfect flowers of these southern populations of *F. paniculata* vary from the type just described for the populations north of Tehuantepec to flowers with very small stigmas held well below the stamens on a short, slender style (Fig. 5b and c).

Field observations were made on several populations of *Fuchsia paniculata* in Costa Rica by Arthur Weston in April, 1971. At one locality in Prov. Cartago, between El Empalme and La Trinidad, a random selection of the population yielded 11 pistillate and 15 perfect-flowered plants. All perfect-flowered plants were found to be functionally staminate, because no developing fruits could be found on them. This agrees with observations in Chiriquí Province of Panama by Woodson & Seibert (1937, p. 196). Examination of herbarium specimens of perfect-flowered individuals from Panama and Costa Rica do show, however, a number of collections with some ripe or developing fruits, for example, *Hammel 3052* (MO) and *Wilbur et al. 13443* (DUKE). In general, however, far fewer fruits are produced on perfect-flowered plants than on pistillate plants in the populations south of the Isthmus of Tehuantepec, and this can be seen easily both in the field and on herbarium specimens. In addition, fewer seeds apparently develop in fruits of the perfect-flowered plants. The perfect flowers are thus largely female-sterile, and the populations south of the Isthmus of Tehuantepec are consequently subdioecious like the three morphologically gynodioecious species of sect. *Encliandra* (Arroyo & Raven, 1975).

Perfect-flowered plants with small stigmas and short styles, raised at the Missouri Botanical Garden from seed of *Breedlove 42742* (MO) from Chiapas, Mexico, regularly produced moderate numbers of selfed fruits with viable seeds. Some of these seeds were raised until flowering, yielding 9 hermaphroditic and 4 pistillate individuals. Although the sample size was quite small, this does indicate that male sterility in *F. paniculata* is not controlled by a dominant gene, as seems to be the case in sect. *Encliandra* (Arroyo & Raven, 1975). The male sterility in sect. *Schufia* may therefore be more similar to that found in the unrelated sect. *Skinnera,* in which it is controlled by a recessive gene (Arroyo & Raven, 1975).

The incomplete female sterility in the perfect-flowered plants of *Fuchsia paniculata* south of the Isthmus of Tehuantepec, the presence of only hermaphroditic populations of the same species north of Tehuantepec, and the presence of an entirely hermaphroditic, closely related species, *F. arborescens,* clearly represents a dynamically evolving progression from hermaphroditic to dioecious plants,

where first male sterility, then female sterility, have been selected to promote increased outcrossing.

Diploid gametic chromosome counts of $n = 11$ were obtained from the following collections of *Fuchsia paniculata*: *Breedlove 5971, 7343,* and *Raven 20995.* In addition, a count of $n = 11$ with normal meiotic pairing was obtained from an experimental cross between two different populations of *F. paniculata,* one from Oaxaca (*Hill 1730,* MO) and the other from Costa Rica (L. Fournier, El Empalme, Cartago; no voucher).

Fuchsia sect. **Fuchsia**. TYPE: *Fuchsia triphylla* L. *Eufuchsia* Baillon, Hist. Pl. 6: 467. 1877, as section. Munz, Proc. Calif. Acad. Sci. IV. 25:15. 1943.

Hermaphroditic. Erect, scandent, or climbing shrubs. Leaves opposite or whorled. Flowers generally pendant; axillary, racemose, or paniculate. Floral tube usually longer than sepals. Petals usually more than ½ the length of the sepals and generally not convolute at anthesis. Nectary annular, surrounding the style and free from the tube except for the basal ½ or less, rarely fully adnate to the floral tube. Stamens biseriate, shorter than the sepals or exserted less than 5 mm beyond them, the antisepalous stamens longer than the antipetalous stamens. Berry with ca. 50–ca. 200 seeds, these compressed laterally, irregularly triangular or obovate in outline, 1–2.5 mm long, 0.7–1.9 mm wide. Gametic chromosome numbers, $n = 11, 22$.

7. Fuchsia boliviana Carrière, Rev. Hort. 48:150, *pl.* 1876. TYPE: *Plate* in Carr., Rev. Hort. 48:150. 1876. Lectotype here designated. The plant illustrated is from garden material cultivated in France, ca. 1876, from seeds collected in the mountains of Bolivia in 1873 by Benedict Roezl. For full synonymy see Berry (1982).

Fuchsia corymbiflora auct. mult., non Ruiz & Pavón. 1802.

Erect, openly-branched shrubs 1.5–4(–6) m tall. Branchlets ascending at base, nodding towards apex, 1–4 dm long, 3–7 mm thick, terete to angled, densely tomentose; older branches and trunks 1–5 cm thick. Leaves opposite, sometimes alternate or ternate, soft-membranous, elliptic to ovate, rounded to acute at base, acute to acuminate at apex, 5–20(–23) cm long, 3–12(–15) cm wide, dark matte green above, paler below, soft pubescent on both surfaces; margin denticulate with numerous glandular teeth; petioles pubescent, 2–5(–7) cm long, stipules dark, filiform, 1–2 mm long, ca. 0.3 mm wide, deciduous. Flowers numerous in terminal, drooping racemes or few-branched panicles, the flowers congested toward the tip; rachis 5–40(–60) cm long; bracts reflexed, lanceolate, 5–25 mm long; pedicels slender, 5–16 mm long; floral tube narrowly funnelform, 30–60(–70) mm long, 1.5–3 mm wide at base, gradually widened above until 5–8 mm wide at rim, pubescent outside, pilose inside; sepals lanceolate, acuminate, 10–20 mm long, 4–5 mm wide, initially spreading but soon becoming fully reflexed, the tips connivent in bud; tube and sepals pale pink to usually bright scarlet; petals red, oblong to lanceolate, acute at apex, 8–16(–20) mm long, 3–7(–9) mm wide, ± crispate with 2–3 longitudinal ridges; petals shrivel and fall off before tube dehisces; nectary annular, 4-lobed, 2–4 mm high, mostly free from the tube; fila-

ments red, the antisepalous filaments 8–15 mm long, the antipetalous filaments 5–10 mm long; anthers oblong, 2–3.5 mm long, 1–1.5 mm thick, white; style red, pubescent, the stigma capitate, subtetragonous, 2–3.5 mm long, 3–5 mm wide, 4-parted at apex, cream. Berry ellipsoid to cylindric, 10–25 mm long, 8–14 mm thick, dark purple, comestible; seeds tan, 1.5–2.0 mm long, 0.5–1.0 mm thick. Gametic chromosome number, $n = 11$.

Distribution: Escaped from cultivation and locally established on moist slopes from Puebla south to Costa Rica, always near habitations. (Native to southern Peru, Bolivia, and northern Argentina.) Flowering throughout the year.

Specimens examined (both naturalized and cultivated): MEXICO, CHIAPAS: Piedracitos, Chamula, *Breedlove 8018* (DS). DISTRITO FEDERAL: Villa Obregón, *Moore 6395* (BH); Coyoacán, *Woronow 2065* (LE). PUEBLA: Huauchinango, *Baldwin 14390* (LL). VERACRUZ: Orizaba, *Botteri 929* (LE); Jalacingo, *Dodds 57* (MO); Altotonga, *Foster in 1938* (BH, BM); Santa Ana Atzacán, N of Orizaba, *Rosas 191* (MO); Santa Cruz, Altotonga, *Ventura 1026* (CAS). GUATEMALA, SACATEPÉQUEZ: San Rafael, *Donnell Smith 2176* (K, US); Antigua, *Standley 62331* (F). SAN MARCOS: Tajumulco, Volcán Tajumulco, *Johnston 1231* (F), *Steyermark 36510* (F). EL SALVADOR: Volcán de San Salvador, *Calderón 2345* (F, US). COSTA RICA, ALAJUELA: Zarcuo, *A. Smith 2775* (F). CARTAGO: Cartago, *Donnell Smith 4804* (US). SAN JOSÉ: San José, *Pittier 14104* (CM, GH, U, US); Guadalupe, *Quiros 1289* (F).

Fuchsia boliviana is perhaps the most widely naturalized species in the genus, at least in tropical and subtropical areas. Outside of its probable native range of southern Peru to northern Argentina, it is also naturalized in Colombia, Venezuela, Jamaica, Hawaii, Java, Réunion, India, and a number of other countries. A single introduced plant can give rise to extensive local populations, because it self-pollinates very effectively and also reproduces vegetatively by stem shoots. Its striking drooping terminal racemes stay in flower through the year, and it is tolerant of much drier and harsher conditions than most species in the genus. For these reasons, *F. boliviana* is a frequently cultivated and escaped shrub in many villages throughout Central America and Mexico. A diploid gametic chromosome count of $n = 11$ was obtained from *Breedlove 8018* (DS).

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APPENDIX

Fuchsia hybrida Hort. ex Sieb. & Voss. in Vilm, Blumengart. 3, 1:332. 1896.

Specimens examined (presumed cultivated): MEXICO, HIDALGO: Real del Monte, *Salazar s.n.* (MEXU). MICHOACÁN: Hacienda Coahuayula, *Emrick 204* (F). PUEBLA: San Pedro, *Nicolas s.n.* (NY). VERACRUZ: Jalapa, *Calzada 2086* (MO); Altotonga, *Dodds 41* (MICH); La Orduña, Municipio Coatepec, *Jiménez 70* (MO); Congregación Dos Pocitos, Municipio Tonayán, *Márquez et al. 456* (MO), *457* (MO), *459* (MO); Casa Quemada, Km 36 of Teocelo road, Cosautlán, *Márquez et al. 965* (MO); Zoncuantla (La Pitaya), Municipio Coatepec, *Murrieta 103* (MO). GUATEMALA, ALTA VERAPAZ: Vicinity of Cobán, *Standley 91231* (F), *92468* (F). GUATEMALA: without locality, *Aguilar 125* (F), *171* (F), *173* (F). HUEHUETENANGO: Wahshaklahung Pyramid, San Mateo Ixtatán, *Breedlove 8658* (DS). SACATEPÉQUEZ: Antigua, *Standley 63836* (F). COSTA RICA, SAN JOSÉ: San José, *Umaña 20* (F).

Fuchsia magellanica Lamarck, Encyc. 2:565. 1788.

Specimens examined (presumed cultivated): MEXICO, PUEBLA: *Arsène s.n.* (US). SAN LUIS POTOSÍ: San Luis Potosí, *Schauffeur in 1879* (A). PANAMA, CHIRIQUÍ: Boquete, *Dwyer 7022* (MO).

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INDEX

Synonyms are italicized. Page numbers of main entries are in bold face, those of illustrations or maps are in italics.

Aglaiocercus kingi 31
Anthracothorax dominicus 31
Araucaria 8
Arracacia incisa 27
Ascidiogyne 26
Berberis 8
Bombus 207
Brebissonia Spach 4, 67
  microphylla Humboldt, Bonpland & Kunth 67
Cactaceae 9
Camissonia arenaria 64
Chlorostilbon swainsonii 31, 51, 190, 191
Chusquea 8
Circaea 4, 30
Clarkia 33, 65
Compositae 26, 28
Drimys 8
Ellobium Lilja 68, 212
  fulgens (DC) Lilja 217
Ellobum Blume 68, 212
Encliandra Zuccarini 68
  parviflora Zuccarini 68
Epilobium 48
Espletia 24
Fuchsia
  Sect. Breviflorae de Candolle 4
  Sect. Ellobium 3, 4, *6*, 7, 9–11, 55, 59, 62, 63, 65, 66, 209, **212–213,** 215, 216
  Sect. Encliandra 3, 4, *6*, 7, 9–11, 33, 59, 66, 181, 209, 210, 231
  Sect. Eufuchsia Baillon 68
  Sect. Fuchsia 2–4, *5*, *6*, 7, 10, 11, 16, 19, 21–23, 59, 66, 209, 210, 212, 214, **232–233**
  Sect. Hemsleyella 1, 3, 4, 5, 7, 9–11, 16, 31, 33, 55, 59, 62, 63, 65, 66, 209, 210, 212, 214
  Sect. Jimenezia 3, 4, *6*, 7, 9–11, 59, 66, 194, 209, 210, **220–221**
  Sect. Kierschlegeria 1, 3–*5*, 7, 9, 10, 11, 33, 59, 65, 181, 200, 209, 210
  Sect. Longiflorae de Candolle 4
  Sect. Macrostemonae de Candolle 4
  Sect. Quelusia 1, 3, 4, *5*–7, 10, 33, 59, 65, 66, 209
  Sect. Schufia 4, *6*, 7, 9–11, 30, 59, 66, 181, 209, 210, **223–224,** 231
  Sect. Skinnera 3, 6, 9–11, 59, 63, 65, 66, 181, 209, 210, 231
  abrupta I. M. Johnston 34, *47*, 53, 57, 78, 79, 80, *105*, **109–110,** 142, 150, 171
  adpressipilis Steyermark 90
  ampliata Bentham 18, 34, 40, *49*, 53, 61, 85, 86, *115*, 122, 124, **125–127,** 146, 176
  andrei I. M. Johnston 34, 53, 56, 104, *105*, **106–108,** 109
  apiculata I. M. Johnston 83, 86
  arborea Sessé & Mociño 211, 223, 224
  arborescens Sims 209–211, 221, 223, **224–227,** *228*, 231
    forma *parva* Munz 228
    forma *tenuis* Munz 228
    var. *megalantha* Donnell Smith 224, 228
    var. *syringaeflora* Lemaire 228
    var. *typica* 224
  asperifolia K. Krause 102
  aspiazui J. F. Macbride 109, 110
  asplundii J. F. Macbride 121
  atrorubra I. M. Johnston 90
  austromontana I. M. Johnston 19, 27, 34, 53, *140*, 141, **142–143**
  ayavacensis Humboldt, Bonpland & Kunth 26, 34, 53, *115*, **121–122,** 125, 126
  boliviana Britton 81
  boliviana Carrière 14–16, 27, 30–32, 34, 54–56, *58*, 59, 61, *63*, 83, **162–170,** 171, 172, 210, 211, 218, 232, 233
  brittonii I. M. Johnston 82
  canescens Bentham 2, 34, 54, 56, 57, 61, 117, 118, 120, 122, 125, 177, **182–184**
  caracasensis Fielding & Gardner 38, 43, 89
  caucana P. Berry 17, 34, 37, 40, *49*, 53, 61, 62, 115, 117, **118–121,** 184
  ceracea P. Berry 34, *51*, 54–56, 58, 59, 110, **149–150,** *151*, 153
  cinerea P. Berry 26, 34, 54, 94, *177*, **184–185**
  coccinea Aiton 67
  cochabambana P. Berry 53, 57, 58, 83, *140*, **144–145**
  colombiana Munz 38, 114, 118
  confertifolia Fielding & Gardner 53, 56–58, *130*, **136–137**
  cordifolia Bentham 209, 211, 212, 216
  coriacifolia P. Berry 54, 57–59, 149, **150–152,** 153
  corollata Bentham 17, 34, 37, 40, 53, 61, 65, 94, 112, **114–118,** 120, 121, 155, 176, 183, 184
  corymbiflora Ruiz & Pavón 34, 54, 58, 78, 110, 142, 150, 156, 162, 168, **170–171,** 172, 175, 176, 211
    alba Harrison 163, 170
    forma *puberulenta* Munz 163
    var. *luxurians* I. M. Johnston 163, 169
  crassistipula P. Berry 16, 34, *46*, 54, 56, 57, *58*, *177*, **181–182**
  cuatrecasasii Munz 24, 39, 53, 56–58, 88, 104, *105*, **108–109,** 155, 194
  curviflora Bentham 111, 114
  cuspidata Fawcett & Rendle 163
  cyrtandroides Moore 9, 28, 33
  decidua Standley 209, 210, 211–213, *214*, **219–220,** 227
  decussata Ruiz & Pavón 27, 52, 56, 58, **76–79,** 80, 81, 110, 142

denticulata Ruiz & Pavón 14, 19, 22, 26, 27, 29, 34, 40, *46*, 53, 55, 59, 61, 62, 78, 80, 83, 110, **137–142,** 143–148, 162, 171, 183
dependens Hooker 14, 15, 35, 54, 58–60, 94, 118, 127, 155, 171, **174–176,** *177*, 178, 180, 184, 185, 218
dolichantha K. Krause 137
dominiana 40, 147
encliandra Steudel 68
excorticata (J. R. & J. G. A. Forster) Linnaeus f. 67
ferreyrae P. Berry 35, *50*, 52, 56, 59, 61, *78*, **79–80,** 81, 110, 142
filipes Rusby 82
fischeri J. F. Macbride 173
fontinalis J. F. Macbride 18, 35, 52, 56, 59, *78*, **80–81,** 172
fosbergii Munz 143, 144
fulgens de Candolle 209, 211–213, *214*, **216–218,** 227
pumila Carrière 217
furfuracea I. M. Johnston 27, 54, 83, *151*, 158, **159–161,** 162, 168
fusca K. Krause 77, 78
gehrigeri Munz 15, 23, 25, 32, 35, 38, 39, 41–43, 53, 56, 61, 89, 92, 113, 129, *130*, **132–135,** 194
glaberrima I. M. Johnston 26, 52, 55–58, *93*, **97–98,** 102, 106
harlingii Munz *49*, 53, 56, 61, *140*, **143–144**
hartwegii Bentham 16, 17, 30, 34, 35, 54–56, 88, 114, 155, 176, *177*, **178–181**
hirtella Humboldt, Bonpland & Kunth 24, 35, 39, 54, 56, 114, 130
hitchcockii I. M. Johnston 122, 124, **176–178,** 179–182, 194
hybrida 211
hypoleuca I. M. Johnston 83, 86
intermedia Hemsley 214, 216
involucrata Sw. 195
jahnii Munz 132, 133
jimenezii Breedlove, Berry & Raven 194, 209, 210, *214*, 220, **221–223**
juntasensis Kuntz 63
killipii I. M. Johnston 127, 129
lampadaria J. O. Wright 147, 148
lehmannii Munz 35, 53, **104–106,** 107–109, 136
leibmanni H. Leveille 228
leptopoda K. Krause 138, 141
llewelynii J. F. Macbride 53, 56, *130*, **135,** 136, 137
longiflora Bentham 145
loxensis Humboldt, Bonpland & Kunth 14, 18, *32*, 35, 52, 56, *65*, **83–86,** *87*, 125, **144**
lycioides Andrews 10, 33, 199–208
macropetala Presl 32, 40, 52, *87*, **99–100,** 101
macrophylla I. M. Johnston 14, 27, 32, 35, 40, 52, 58, 60, *87*, **98–99,** 100–102
macrostigma Bentham 18, 25, 40, 53, 58, 61, 62, 88, 94, *140*, **145–147**
var. *longiflora* (Benth.) Munz 145
var. *pubens* I. M. Johnston 145
magdalenae Munz 22, 24, 28, 35, 53, 56, 61–*63*, 65, *140*, **147–148**
magellanica Lamarck 10, 67, 211
mathewsii J. F. Macbride 18, 26, 35, 54, 56, 59, 81, *156*, 168, 172, **173–174**
meridensis Steyermark 127
microphylla Humboldt, Bonpland & Kunth 68, 206
miniata Planchon & Linden 194
munzii J. F. Macbride 170, 171
nigricans Linden ex Planchon *13*, 15, 30, 32, 35, 36, 38, 41–44, *47*, *51*–53, 55, 59, 61, **89–92,** *93*, 95, 104, 114, 130, 134, 155, 194
orientalis P. Berry 18, 36, 52, 57, 88, *93*, **95–97,** 98
osgoodii J. F. Macbride 106, 108
ovalis Ruiz & Pavón 52, 57, 59, *87*, 99, **100–101,** 102, 108
var. *aberrans* J. F. Macbride 106, 108
pallescens Diels 18, 36, 52, 55, 58, 61, 88, 91, *93*, **94–95,** 104, 125
paniculata Lindley 30, 209–211, 223, 224, *225*, **227–232**
perbrevis I. M. Johnston 193
petiolaris Humboldt, Bonpland & Kunth 14, 16, 24–26, 36, 52, 53, 55, 61, 85, **110–114,** *115*–118, 120, 122, 124, 126, 130, 133, 178
var. *bolivarensis* Munz 111
pilosa Fielding & Gardner 36, 52, 53, 55–57, 59, 61, *64*, *87*, 97, **101–103,** 132, 137, 172
platypetala I. M. Johnston 38, 194
polyantha Killip ex Munz 26, 32, 36, 48, 54, 56, 58, 94, **155–157**
polyanthella I. M. Johnston 100
pringsheimii 14, 28, 31, 36, 37, 39, 40, *50*, 54, 58, 61–63, 65, *187*, 189, 190, **191–192,** 194
putumayensis Munz 18, 44, 53, 56, 58, 59, 61, *64*, *65*, 92, 95, **103–104,** *105*–107, 109, 110, 147
quinduensis 110, 114
racemosa Lamarck 186, 188
racemosa Sessé & Mociño 217
regia (Vandelli) Munz 67
rivularis J. F. Macbride 36, 53, 55, 56, 61, 102, 103, 129, *130*, **131–132,** 135
sanctae-rosae Kuntz 19, 27, 36, 38, 52, *78*, **81–83,** 142, 145, 159–162, 170
sanmartina P. Berry 54, 78, 80, 149, *151*, **152–153**
scabriuscula Bentham 18, 24, 39, *47*, 52, 56, 57, 62, 85, **86–88,** 94, 95, 97, 109, 147, 155, 194
scandens K. Krause 76
scherffiana André 53, *130*, **136**
serratifolia Ruiz & Pavón 138
sessilifolia Bentham 24, 32, 36, 39, 43, 48, 54, 56–59, 61, 62, 88, 92, 94, 109, 118, 127, 147, **153–155,** 156, 157, 176, 194
simplicicaulis Ruiz & Pavón 27, 54, 59, 60, **148–149,** 150, *151*, 153
siphonata K. Krause 138
smithii Munz 111, 113

spectabilis Hooker ex Lindley 145
splendens Zuccarini 209, 211, 212, **213–216**
steyermarkii P. Berry 26, 52, 57, 58, 85, 87, **88–89,** 136
storkii Munz 173
sylvatica Bentham 18, 25, 36, 52, 57, 88, 90, 91, **92–94,** 95, 96, 147, 155
syringaeflora (Lem.) Carrière 227
tacsoniiflora K. Krause 138, 140
thymifolia Humboldt, Bonpland & Kunth 68, 206
tincta I. M. Johnston 19, 27, 36, 40, 54, 55, 58, 83, 141, *151,* **157–159,** 160–162
townsendii I. M. Johnston 121
triphylla Linnaeus 14, 28, 31, 33, 37, 39, 40, *50,* 51, 54, 55, 58, 59, 65, 66, **185–191,** 192
tuberosa 141
umbrosa Bentham 83, 85
vargasiana Munz ex Vargas 19, 27, 36, 40, 54, 55, 83, 141, *151,* 158, 160, **161–162**
velutina I. M. Johnston 170
venusta Humboldt, Bonpland & Kunth *12,* 15, 16, 24, 36, 39, 41, 42, *49,* 50, *51,* 53, 55, 56, 61, 65, 92, 114, **127–130,** 132–137, 178–180, 194
var. *huilensis* Munz 127
verrucosa Hartweg 25, 30, *32,* 37, 39, 41, 50, 54, 55, *57–59,* 61–*63,* 65, 88, 92, 109, 130, 134, 155, *166,* 178, **192–194**
var. *tamaensis* Steyermark 193
vulcanica André 14, 18, 37, 40, 53, 65, 95, **122–125,** 126, 127
weberbaueri K. Krause 82
woytkowskii Munz 131
wurdackii Munz 18, 37, 54, 57, 59, 102, 137, *156,* 168, 171, **172**
Gongylocarpus 65
Gunnera 95
Hauya 55
Ilex 8
Kierschlegeria Spach 68
lycioides (Andrews) Spach 68
Kirschlegeria H. G. L. Reichenbach 68
Laestadia 28
Laurelia 8
Lepechinia 8
Loasaceae 9
Lopezieae 33
Ludwigia 2–4, 55
Lyciopsis Spach 4, 68
thymifolia (Humboldt, Bonpland & Kunth) Spach 68
Mellisuga minima 31
Monochaetum 48
Myrinia Lilja 68
microphylla (Humboldt, Bonpland & Kunth) Lilja 68
Nahusia Schneevoogt 67
coccinea (Aiton) Schneevoogt 67
Nothofagus 8, 10
Nyctaginaceae 9
Ocreatus underwoodii 31
Oenothera 32, 48
Onagreae 33
Perezia 8
Podocarpus 8
Puya 24
Quelusia Vand. 67
regia Vand. ex Vellozo 67
Quilusia J. D. Hooker 68
Rhodopsis vesper atacamensis 201, 204, 206, 207
Rubiaceae 57
Schufia Spach 4, 68, 223
arborescens (Sims) Spach 68, 224
Skinnera J. R. & J. G. A. Forster 67
Spachea Juss. 68, 212
Spachia Lilja 212
fulgens (DC) Lilja 68, 217
Thilcum Molina 67
tinctorium Molina 67
Tilco Adanson 67
Zygophyllaceae 9

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. 68, No. 4, pp. 505–686, was published on 29 March 1982.

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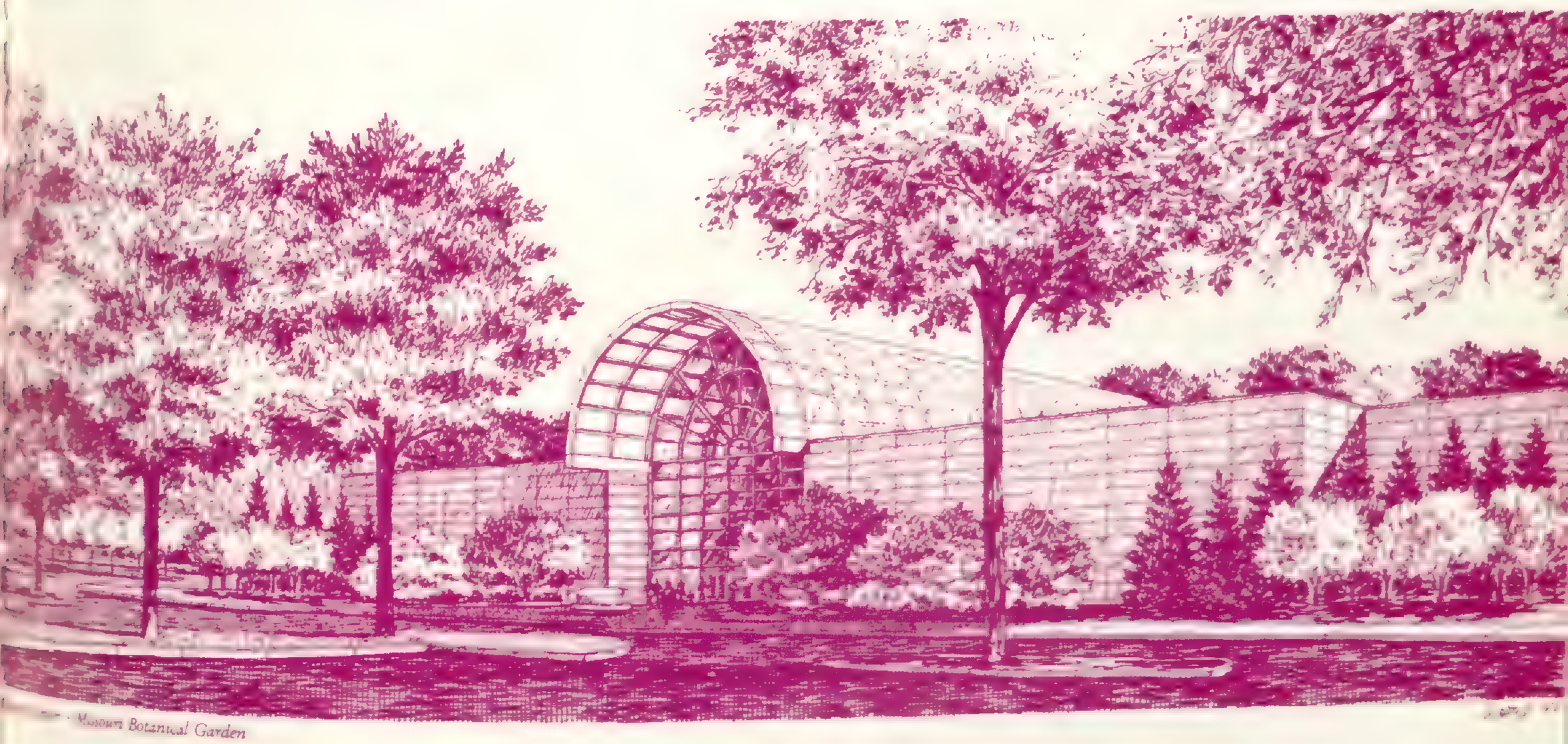

Missouri Botanical Garden

CONTENTS

The Systematics and Evolution of *Epilobium* (Onagraceae) in South America *James C. Solomon* ---- 239

A Revision of the Southwestern Species of *Amsonia* (Apocynaceae) *Steven P. McLaughlin* ---- 336

A Synopsis of *Moraea* (Iridaceae) with New Taxa, Transfers, and Notes *Peter Goldblatt* ---- 351

Corm Morphology in *Hesperantha* (Iridaceae, Ixioideae) and a Proposed Infrageneric Taxonomy *Peter Goldblatt* ---- 370

Notes on *Geissorhiza* (Iridaceae): The Species in Madagascar *Peter Goldblatt* ---- 379

Illinois Solanaceae in the Missouri Botanical Garden Herbarium and Biographical Sketches of Some Collectors *Robert H. Mohlenbrock* ---- 382

VOLUME 69
1982
NUMBER 2

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OF THE
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THE SYSTEMATICS AND EVOLUTION OF *EPILOBIUM* (ONAGRACEAE) IN SOUTH AMERICA[1]

JAMES C. SOLOMON[2]

ABSTRACT

Recent field, cytological, experimental hybridization, and morphological studies indicate that the patterns of diversity in South American species of *Epilobium* can best be understood by recognizing 12 native species. These have been derived from at least five independent pre-European introductions of *Epilobium* into South America, with subsequent diversification in some of these lines. Two groups have ancestral affinities with North America: *Epilobium ciliatum* ssp. *ciliatum* is consubspecific with North American populations; the primarily northern Andean group, consisting of *E. denticulatum* and allied species, has no close relatives in the Northern Hemisphere, but has a chromosomal arrangement identical with that of some North American species. Two other lines are derived directly from Australasian ancestors: *Epilobium hirtigerum* is conspecific with a widespread species of Australia and New Zealand, and *E. conjungens*, with its unusual creeping habit and consistently opposite

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leaves, is closely allied to *E. brunnescens* ssp. *brunnescens* of New Zealand. Progenitors of these species presumably arrived by long-distance dispersal via the prevailing westerlies. The remaining species are southern South American, and show no close affinities with species found in other geographical areas. Fertility data from experimental hybrids suggest a close alliance between some of the morphologically distinct species in this group. Their precise relationships, however, and the origin of possible ancestors, remains obscure, although Australasia appears to be the most likely source. Three other species have been introduced into South America in historical times, two from Europe and one from North America.

Epilobium, the largest genus in the Onagraceae, comprises approximately 185 species distributed worldwide in temperate zones on every continent except Antarctica. In tropical regions the species are restricted to temperate montane habitats. Many species are extremely variable and widespread, while others are highly restricted. In general, the genus has been characterized as "taxonomically difficult."

During the last 20 years, a steadily growing number of papers have been published that provide modern treatments for the species of *Epilobium* encountered in Europe (Raven, 1968), Africa (Raven, 1967b), parts of western Asia (Chamberlain & Raven, 1972; Raven, 1964) and eastern Asia (Hara, 1965; Raven, 1962, 1967a), Australasia (Raven & Raven, 1976), and North America (Munz, 1965; Hoch & Raven, 1981b). With the exception of some large parts of continental Asia, the only region without a recent treatment is South America.

Prior to the present study, the only papers dealing specifically with *Epilobium* in South America were those by Samuelsson (1923, 1930). Carl Haussknecht (1884) produced a monograph of worldwide scope, which is still the only comprehensive treatment available. Samuelsson discussed a species only when new specimens amplified or diverged from the limits given by Haussknecht; he described new taxa based on new interpretations of morphology or material collected since Haussknecht's time. In several places Samuelsson pointed out the difficulty of separating some of the taxa he recognized, including some of his new ones, and this suggested that there were a number of taxonomic problems among the South American species of this genus.

Since the early 1920s a substantial quantity of new herbarium material has become available, amounting to many times more than Samuelsson had for study. During these same intervening years, there have been fundamental changes in our concept of the kinds of units that should be regarded as species. A reassessment of the South American species of *Epilobium* in the light of these concepts was viewed as necessary to bring the species into conformity with the approach and philosophy used by Raven & Raven (1976) and Hoch (1978).

Equally important are recent chromosomal studies (Seavey, 1972; Seavey & Raven, 1977a, 1977b, 1977c, 1978; Hair, Raven & Seavey, 1977), especially a preliminary survey of South American plants (Seavey & Raven, 1977c), in which it was suggested that, based on morphology and the distribution of chromosomal end arrangements, the *Epilobium* species in South America may have been derived from ancestors from both North America and Australasia. In order to understand the implications of this interesting biogeographical problem, it was first necessary to delimit taxa that were present in South America. Once the taxa were

circumscribed, additional studies would provide some understanding of the interrelationships among them.

The following questions were kept in mind as this study progressed: How many taxa would it be useful to recognize? Did populations exhibit morphological patterns that had a geographical basis or did the same patterns appear numerous times in different areas? Are the taxa sympatric; do they hybridize, and, if so, what role has hybridization played in the differentiation of natural populations? Where did the taxa originate? What is their relationship with each other, and what impact did historical/geological processes have on their evolution and current distribution? An attempt has been made to answer these questions in greater or lesser detail, depending on the data that could be brought to bear on the subject.

Materials and Methods

An extensive field examination was made of hundreds of populations in the central and southern Andes of Argentina and Chile, and in the altiplano of Bolivia. To supplement the field observations, nearly all of the available herbarium specimens representing the genus in South America were studied.

Seeds collected in the field, from herbarium specimens, or provided by correspondents, were grown in greenhouses at the Missouri Botanical Garden for observation. All plants grown from a single seed source, which may be one or more plants from one collection, are here defined as a strain. Many strains were used in making additional experimental hybrids to expand the studies reported by Seavey & Raven (1977c). These were examined cytologically. Buds were fixed in 1:3 acetic alcohol, hydrolyzed in 1 N HCl for 10–15 minutes at 60°C, stained in acetocarmine and squashed for chromosome observations. In addition, a measure of pollen fertility in the experimental hybrids and suspected natural hybrids was obtained using the malachite green-acid fuchsin-orange G stain of Alexander (1969). Two buds (or flowers, if buds were unavailable) were selected from each plant, pollen from each bud was stained and 100 tetrads scored for aborted and nonaborted grains. The scores for filled grains from the two buds were averaged to give a percentage of stainable pollen for each plant. Generally, two or more individuals of each artificial hybrid strain were averaged to arrive at the figures presented. In some instances, if only one bud was available, the percentage for that bud alone was used, or if there was a striking disparity between the two scores, the higher one was used, since it represents a potential fertility under good conditions.

Generic Relationships

Epilobium is one of two genera currently recognized in the tribe Epilobieae. This tribe differs significantly from the six other tribes of the family Onagraceae in that it has minute, heteropycnotic chromosomes (Kurabayashi et al., 1962); sheds pollen, in most species, as tetrads; has gametic chromosome numbers of $n = 9$, 10, 12, 13, 15, 16, 18, and 19, and multiples of some of these numbers; and occurs primarily in moist or seasonally moist habitats (Raven, 1976).

In addition to *Epilobium*, Epilobieae contains the genus *Boisduvalia*, which is represented in western North America by five species, one of which is shared with South America, and a sixth species endemic to South America (Raven & Moore, 1965). Although *Boisduvalia* is clearly closely related to *Epilobium*, it differs in having an annual habit (only three species of *Epilobium* are annual); angular-fusiform seeds without a terminal coma (Seavey et al., 1977); and chromosome numbers of $n = 9$, 10, 15, and 19. Only $n = 15$ is shared with five species of *Epilobium*, but they have been derived independently of *Boisduvalia* (Raven, 1976).

Epilobium itself is clearly delimited, although two genera, *Zauschneria* and *Chamaenerion*, are often segregated from *Epilobium*. Including these groups, *Epilobium* consists of six well defined sections (Raven, 1976). Section *Cordylophorum*, with three species, and sect. *Zauschneria*, with two, are closely related, share a number of morphological features, and have a base chromosome number of $x = 15$. Polyploidy is known in some subspecies of *E. canum* (Greene) Raven (sect. *Zauschneria*). Two other sections contain the only annual species in the genus, two in sect. *Crossostigma* and one, *E. paniculatum* Nutt. ex Torr. & Gray, in sect. *Xerolobium*. These sections are characterized by unusual morphologies and the chromosome numbers, $n = 13$ or 16 and $n = 12$, respectively. The center of distribution for these four sections lies in western North America. A fifth, very distinctive, group is sect. *Chamaenerion*. Unlike the preceding four sections, the center of distribution for the seven species of sect. *Chamaenerion* is in Eurasia, with only two, *E. angustifolium* L. and *E. latifolium* L., occurring in North America. Section *Chamaenerion* has a base chromosome number of $x = 18$, with polyploids known only in *E. angustifolium* and *E. latifolium*.

The sixth section, sect. *Epilobium*, accounts for the bulk of the genus. The five sections enumerated above contain only 15 species out of a total of approximately 185, leaving about 170 in sect. *Epilobium*, all of which have a gametic chromosome number of $n = 18$. These are widely, but unevenly, distributed in moist, open habitats throughout the temperate regions of the world. For example, Eurasia has more than 70 species, but Africa has only 11, with seven of these shared with Eurasia. There has been a remarkable radiation of this section in New Zealand unparalleled elsewhere in the world, resulting in 37 species, of which 31 are endemic and the remainder shared with Australia. The most primitive member of sect. *Epilobium*, *E. rigidum* Hausskn., is found in western North America, where four of the other sections are also restricted. This pattern of distribution, along with the great morphological and chromosomal diversity exhibited by these sections, leads to the conclusion that *Epilobium* probably originated in western North America (Raven, 1976).

The native South American species are all members of sect. *Epilobium*. In the present treatment 12 native species are recognized. These are distributed along the length of the Andes from Costa Rica, northern Venezuela and Colombia to Cape Horn, except for *E. hirtigerum*, which is restricted to eastern Argentina, Uruguay, and southern Brazil. The greatest concentration of species is found in the central and southern Andes of Argentina and Chile. In addition, three other species have been introduced and persisted or become naturalized in historical times. *Epilobium obscurum* and *E. tetragonum* subsp. *lamyi*, from Europe, are also

members of sect. *Epilobium*. The third species, *E. paniculatum* (sect. *Xerolobium*) has been introduced from North America. A fourth species, *E. angustifolium*, representing sect. *Chamaenerion*, has been collected once in Chile (Valdivia, Valdivia Prov., Chile, *Calvert in 1914*, BM). If this specimen is correctly labeled, then the plant was probably cultivated and has failed to persist or become naturalized. In the absence of additional information, it has been excluded from further consideration.

Haussknecht (1884) grouped the species of *Epilobium* into assemblages based on stigma lobing, seed shape, and other conspicuous morphological features. Samuelsson (1923) maintained these groups for the South American species as outlined by Haussknecht and created two additional ones by removing the taxa allied to *E. australe* from the Platyphylla, placing them in his Australia, and by segregating *E. nivale* and *E. fragile* as Nivalia. Although Haussknecht's categories did bring together species of similar morphologies, the arrangement of the groups and some of their component species do not reflect our current understanding of the genus. Until a much more detailed understanding of the reticulate morphological patterns seen in sect. *Epilobium* is acquired, it does not seem warranted to recognize any assemblages such as those proposed by Haussknecht.

Morphology

In dealing with the South American species of *Epilobium* sect. *Epilobium*, a variety of morphological characters have been useful in delimiting the species, especially habit, perennating structures, pubescence, leaf shape, dentition and arrangement, and seed shape and surface features.

Habit. Epilobiums in South America exhibit a diverse array of habit and growth form. Some species have erect or ascendent stems (e.g., *E. ciliatum, E. glaucum*); others are lax or decumbent (*E. nivale*), and often caespitose (*E. densifolium, E. fragile, E. nivale*). Perhaps the most unusual growth form is that of creeping stems, rooting along their length and with flowers arising from subterminal nodes, characteristic of *E. conjungens*. This habit is shared only with a number of species from Australasia (Raven & Raven, 1976).

All the species in sect. *Epilobium* are perennial herbs. They produce a variety of perennating parts for vegetative reproduction and persistence during the winter. All of the South American species will germinate, flower, and set seed during a single growing season, so it is potentially possible for them to be facultatively annual. This does not, however, seem to be an important factor except, perhaps, in those species that show the greatest tendency to weediness (e.g., *E. ciliatum*).

There are very great differences in branching patterns, from simple to profusely branched. This trait is so variable within species or even populations, however, and so strongly influenced by the age of the plant and the microclimatic conditions under which it grows, that it is of little taxonomic value.

In the Northern Hemisphere, a wide variety of highly specialized perennating structures has evolved, including compact underground buds with fleshy, imbricate cataphylls (turions), leafy rosettes, rhizomes, corms at the tips of thin stolons, and leafy soboles or shoots. Only *Epilobium ciliatum*, of the native South American species, produces turions or leafy rosettes, usually toward the end of

a growing season. In general, the other species are less specialized in this respect, reproducing vegetatively by buds at or near the ground surface or by more or less elongated leafy shoots from the bases of the stems. The leafy shoots in *E. barbeyanum* often take the form of runners 20 cm or more long. Two species, *E. australe* and *E. glaucum,* produce short or elongate scaly rhizomes just under the ground surface, which, in the case of *E. glaucum,* may be up to 20 cm long. These various modes of perennation generally result in clumped groups of stems, although solitary, single-stemmed individuals can be found in many species. *Epilobium ciliatum* is usually solitary, since each plant produces only one or two turions or rosettes, which give rise to the following year's plant. As previously mentioned, *E. conjungens* is quite unusual among the South American species. Its stems form small mats of repent branches, a habit that has apparently evolved through the suppression of the main shoot with a concomitant proliferation of basal shoots (Raven & Raven, 1976).

A conspicuous feature of two of the clumped, caespitose species, *E. densifolium* and *E. fragile,* is the thick, woody, often elongate rootstock. This is in striking contrast to the normally fibrous root system produced by other species.

Pubescence. There are four basic types of hairs found among the species under consideration. The presence or absence of each type has been very useful, either alone or in combination with other characters, in separating taxa. Two species, *E. glaucum* and *E. nivale,* are conspicuous by the absence of pubescence of any type, and the often blue-glaucous, waxy bloom in the former. Very rare glabrous individuals of *E. ciliatum* have been seen, but normally this species is pubescent.

1. Strigillose. Hairs of this type are sharp-pointed, appressed, or at least falcate, upwardly curved, and typically 0.1–0.2 mm long. Following Raven & Raven (1976) and Hoch (1978), these hairs have been termed strigillose. This is by far the most common pubescence type found in *Epilobium.* The density and distribution of strigillose hairs varies considerably within and between species, but they are found in nearly all species except for the glabrous ones mentioned above. There is some variation in how closely appressed the strigillose hairs are on an individual plant. Often the hairs on the ovaries are closely appressed, while those elsewhere on the plant are more spreading.

In *E. puberulum* the basic strigillose hair type is generally longer, ranging from 0.15 to 0.4 mm, and often somewhat spreading. A second modified hair type occurs in *E. conjungens.* In this species the hairs are much smaller, 0.02–0.08 mm long, and often curled in dried specimens. It is not known if these hairs are straight in living plants, but because they are distinctive, this type of pubescence has been termed puberulent.

2. Glandular. These hairs are more or less appressed to erect, blunt-tipped, 0.1–0.2 mm long. In living plants each hair usually exudes a minute droplet of liquid. When they are sufficiently abundant, as in *E. barbeyanum* and some populations of *E. ciliatum,* the entire plant may feel moist or viscid to the touch. Normally, when dried, these hairs become flat and twisted with an evident rounded tip. Glandular hairs are absent in *E. australe, E. densifolium, E. puberulum,* and *E. conjungens.* In the other species their density and distribution vary con-

siderably, but they are generally present in the inflorescence, on the ovaries and floral tube, and along the margins of young leaves.

3. Long, erect. A distinction is made here between two types of erect hairs that are each restricted to a single species. The long, very fine, soft, erect hairs found in *E. hirtigerum* measure between 0.25 and 0.6 mm long and are designated as villous.

A number of populations of *E. denticulatum* from southern Peru and western Bolivia contain plants that were described by Samuelsson (1923) as *E. hirtum*. These are characterized by long erect or spreading hairs, 0.2–0.4 mm long, which are here termed hirsute. Long hairs of this type intergrade continuously with the slightly shorter strigillose pubescence mentioned earlier, both in length of the hairs and in the degree to which they are appressed.

4. Appressed, blunt-tipped. These are generally small, 0.05–0.1 mm, blunt-tipped hairs that are tightly appressed to both surfaces of the leaf blade. They have been found in only *E. denticulatum* and *E. pedicellare*. The distinction between these hairs and the glandular ones discussed earlier is very fine. The appressed hairs are smaller but merge imperceptibly with the glandular ones in the region of the petiole and lower leaf blade. In living plants, the appressed hairs never produce an exudate. Older leaves are often glabrate, so the appressed hairs may be found only on the younger leaves. In plants of *E. denticulatum* that are hirsute, the hairs on the leaves may also be erect, and are perhaps under the same type of genetic control.

Leaves. The basic leaf type found in South American species is lanceolate, thin, and acute at the apex. In a few instances, however, species deviate from this shape sufficiently for the leaf outline to be a useful taxonomic character. Ovate, thick leaves are typical in *E. australe,* and elliptic to orbicular blades are found in *E. conjungens*.

The type and size of teeth on the leaf margins can also be helpful. The majority of species have few, denticulate teeth. In contrast, the margins of leaves in *E. ciliatum* are usually serrulate with numerous teeth. *Epilobium pedicellare* is quite unusual in having leaves with coarsely serrate margins, the teeth of uneven sizes. The few, narrow, sharply pointed, forward-directed teeth in *E. hirtigerum* are also diagnostic. These last two species are also distinctive in their mostly alternate leaves. Other species normally have opposite leaves, or leaves that are alternate only in the inflorescence.

Inflorescences. Inflorescences in *Epilobium* are only partially useful as a diagnostic feature. They may vary from simple to paniculate and densely branched. The nature of the inflorescence depends upon the branching pattern exhibited by the individual plant. In general, inflorescences are terminal, erect, and highly variable in the total number of flowers produced during a growing season. Each branch of the inflorescence normally presents only one or a few flowers each day, which only last for that given day. As an example, *E. densifolium* seldom produces more than five or six flowers per stem during an entire season. A single plant, however, may bear many more flowers than this because of its densely branched caespitose habit. Flower production in other species is usually much

more prolific. For example, a large plant of *E. ciliatum* may produce several hundred or more flowers in a single season. The nodding inflorescence and flowers of *E. denticulatum* are very characteristic, although this feature may be lost in preparing specimens or if the plants are collected very late in the growing season. *Epilobium conjungens* exhibits one of the most specialized inflorescence types in *Epilobium*. Instead of producing a discrete, terminal, several-flowered inflorescence, it bears only a few flowers singly along the stem, which continues to grow and root at the tip.

Flowers. Most South American species have flowers with petals of varying shades of pale pink to rose purple. White, or nearly white, petals are found in *E. hirtigerum*, *E. conjungens*, many populations of *E. ciliatum*, and occasionally in *E. denticulatum*. *Epilobium puberulum* is unique in having salmon pink petals. Flower size, color, and morphology alone are generally not sufficient to separate any species but are useful in combination with other characters. The only exception to this is *E. puberulum*, which has a very distinct morphology as well as petal color. At anthesis the petals of *E. puberulum* are imbricate and each one is bent at about 90° a short distance above its insertion on the floral tube. Thus, the four petals produce a flat plane at right angles to the axis of the floral tube, with a small circular opening formed by the bends in the petals. The stigma is positioned in this opening at about the same level as the bend in the petals, with the dehisced anthers of the four longer stamens pressed between the stigma and the petal bend. The four antipetalous stamens have extremely short filaments, usually less than 0.6 mm long, much shorter than in any other species.

Among the other species, there is considerable variation in petal size, with certain ranges characteristic of a few species, such as *E. densifolium*, which has very large petals, but the magnitude of overlap and the variability of some species precludes the use of flower size by itself as a taxonomic character.

Another unique floral feature is the lavender or bluish staminal filaments found in *E. denticulatum* and *E. pedicellare*. Additional notes on floral features are discussed under floral biology.

Seeds. The morphology of seeds has been considered a useful feature in the taxonomy of *Epilobium* for a very long time (e.g., Haussknecht, 1884; Samuelsson, 1923). Within recent years several surveys of seed surface morphology using scanning electron microscopy have been conducted by Berggren (1974), Raven & Raven (1976), Hoch (1978), and Seavey et al. (1977). The last study is of particular importance because it is a worldwide survey of all the sections and includes species from all the continental areas where *Epilobium* occurs.

Three basic types of seed surfaces are recognized by Seavey et al. (1977). *Papillose:* each cell has a more or less prominent, regular or irregular convex portion in the center of the cell. *Ridged:* this is a specialization of the papillose type in which the papillae are flattened laterally and fused or nearly fused end-to-end in longitudinal rows to form ridges. *Reticulate:* the surface cells show only a regular polygonal reticulum formed by the radial walls, without a papilla.

Nearly all of the species of *Epilobium* in South America have papillose seed surfaces, which is the typical surface morphology for the majority of species in

section *Epilobium* (Seavey et al., 1977). Four species have been illustrated in Seavey et al. (1977): *E. denticulatum* (Figs. 64–66; as *E. hirtum,* Figs. 73–75), *E. australe* (as *E.* sp., Figs. 70–72), *E. densifolium* (as *E.* cf. *pauciflorum,* Figs. 61–63), and *E. glaucum* (Figs. 67–69), and a fifth, *E. hirtigerum* in Raven & Raven (1976, Fig. 3b). These examples represent the full range of papillose seeds found in South America.

Epilobium ciliatum is the only species in South America that has nonpapillose seeds. This species produces conspicuously ridged seeds, a type known only in *E. ciliatum* and the relictual western North American *E. oreganum* Greene, both members of the *E. ciliatum* complex (Hoch, 1978). Seeds from South and North American populations are illustrated in Seavey et al. (1977, Figs. 169–174). Foveolate cells are also found on the seeds of *E. ciliatum,* but such seeds do not characterize any distinct taxonomic group. Some populations of *E. ciliatum* from southern Patagonia and Tierra del Fuego may have at least part of the upper seed surface with a reticulate pattern. The area covered by foveolate cells varies in size, but the seeds always have longitudinal ridges along the sides and at the micropylar end. This situation is somewhat analogous to that reported by Hoch (1978) for some populations of *E. ciliatum* subsp. *glandulosum* but has not proceeded to the complete elimination of the ridges.

Seed length is variable, ranging from 0.7 to 2 mm, and is somewhat useful as a diagnostic feature. The majority of species have seeds between 0.8 and 1.4 mm long, with substantial variation within species. *Epilobium puberulum* has consistently small seeds, 0.7–0.9 mm long, and *E. densifolium* has the largest seeds, 1.4–2 mm long. Except for the largest seeds of *E. densifolium,* seed size overlaps too broadly to be used alone to separate taxa.

An additional useful character is the short, often rather broad, pellucid chalazal appendage found in six species, *E. ciliatum, E. denticulatum, E. pedicellare, E. fragile, E. puberulum,* and *E. nivale* (cf. Seavey et al., 1977; Hoch, 1978).

Cytogenetics and Crossing Relationships

Cytogenetics. All of the species of *Epilobium* sect. *Epilobium* that have been examined cytologically have a gametic chromosome number of $n = 18$. Numbers for South American species, some of which are reported here for the first time (Table 1), conform to this pattern, which is based on studies of hundreds of strains from all parts of the world (e.g., Seavey & Raven, 1977a, 1977b, 1977c). Chromosomes in *Epilobium* are uniform in morphology. At meiotic metaphase I they are small (2–4 μm long), heteropycnotic, and exhibit no evident karyotypic markers; they are indistinguishable from one another.

In 1968, Mosquin found evidence for reciprocal translocations while examining chromosomal pairing in experimental hybrids between several species. These initial results have been elaborated on considerably by Seavey (1972), Seavey & Raven (1977a, 1977b, 1977c, 1978), and Hair, Raven, & Seavey (1977), so that the number and distribution pattern of reciprocal translocations in section *Epilobium* is now known in some detail.

Three major species groups, which account for nearly all species in sect. *Epilobium,* have been detected on the basis of reciprocal translocation differ-

TABLE 1. Chromosome numbers in South American species of *Epilobium*. All strains formed 18 bivalents in meiosis. Vouchers are deposited at the Missouri Botanical Garden (MO) unless otherwise indicated. Full localities listed under respective species.

E. australe. Chile, *Marticorena et al. 475, 834*.
E. barbeyanum. Chile, *Solomon 4285, 4296*.
E. ciliatum subsp. *ciliatum*. Argentina, *Solomon 4712*. Chile, *Eyerdam 10296* (NY); *Marticorena et al. 852, 970*; *Moore 412* (LA).
E. denticulatum. Bolivia, *Solomon 4938*. Ecuador, *Berry 2522*; *Weydahl 153* (S).
E. glaucum. Chile, *Marticorena et al. 441, 991*.
E. hirtigerum. Argentina, *Krapovickas & Cristóbal 14675*.
E. nivale. Argentina, *Gentili in 1975*.
E. obscurum. Chile, *F. Schlegel 6882*.
E. pedicellare. Bolivia, *Solomon 5147*.
E. puberulum. Chile, *Marticorena et al. 1015*; *Moore 296* (LA).

ences. The chromosomal arrangements that characterize each group have been given the arbitrary designations of AA, BB, and CC (Seavey, 1972; Raven, 1972). Hybrids within chromosomal groups produce 18 pairs of chromosomes at meiotic metaphase I, but those between groups produce various combinations of pairs and rings and/or chains.

The BB arrangement is considered to be the ancestral condition in sect. *Epilobium* for the following reasons. First, one of the two most primitive species in section *Epilobium*, *E. obcordatum* A. Gray from western North America (Raven, 1976), has this arrangement. Second, the other two arrangements, AA and CC, each differ from the BB by a single reciprocal translocation. AA and CC differ from each other by two overlapping reciprocal translocations. Thus, hybrids between plants with the AA and CC arrangements have 15 pairs and a ring or chain of 6 chromosomes at meiotic metaphase I, while hybrids between plants with the AA or CC arrangements and those with the BB arrangement produce 16 pairs and a ring or chain of 4. The simplest hypothesis for the derivation of these chromosomal groups is that the AA and CC arrangements were each derived independently from the BB arrangement. Third, the BB chromosome arrangement characterizes the largest number of species in sect. *Epilobium* and is the most widespread of the three. It is the common arrangement in Eurasia and Africa and the only one found in Australasia. A number of South American species have this arrangement, and it distinguishes a large group of species in North America.

The AA arrangement is primarily restricted to the New World, where it is known from the *E. ciliatum* complex, consisting of five species centered in western North America, several species in South America, and three apparently unrelated species in Europe, *E. alpestre* (Jacq.) Krock., *E. alsinifolium* Vill., and *E. atlanticum* Litard. & Maire, the latter also found in the Atlas Mountains of Morocco.

The third arrangement, CC, is found in a series of closely related, circumboreal species, including *E. hornemannii* Reichenb., *E. anagallidifolium* Lam., and *E. clavatum* Trel., among others. Also found to have the CC arrangement is the distinctive western North American species *E. luteum* Pursh, which has four-lobed stigmas and cream-colored flowers.

Besides these three arrangements, two additional unique ones have been dis-

TABLE 2. Strains of *Epilobium* used in artificial hybridization experiments. Vouchers deposited at MO; full collection information given under respective species. Acronyms and strain letters are those used in Tables 3 and 4, and Figures 1 and 2. If the name given in Seavey and Raven (1977c) differs from the nomenclature used here, that name has been placed in parentheses after the corresponding strain.

E. australe. (AUST)
(a) Argentina, *Moore 1686* (*E.* sp.).
(b) Chile, *Marticorena et al. 834*.
(c) Argentina, *Rubulis in 1976*.
E. barbeyanum. (BARB)
Chile, *Solomon 4296*.
E. ciliatum subsp. *ciliatum*. (CIL)
Chile, *Zöllner 7868* (*E. chilense* Hausskn.).
E. ciliatum Raf. subsp. *watsonii* (Barbey) Hoch & Raven. (WAT)
U.S.A., California, *Sharp in 1967* (*E. watsonii* Barbey).
E. densifolium. (DENS)
(a) Chile, *Zöllner 6245* (*E.* cf. *pauciflorum* F. Phil.).
(b) Argentina, *Diem 3600*.
E. denticulatum. (DENT)
(a) Argentina, *Hunziker & Ariza 20424*.
(b) Perú, *Conrad 2715*.
(c) Perú, *Averett 1004* (*E. hirtum* Samuelsson).
E. glaucum. (GLAU)
(a) Chile, *Marticorena et al. 7*.
(b) Chile, *Marticorena et al. 951*.
E. hirtigerum. (HIRTIG)
(a) New Zealand, *Raven 25148*.
(b) Argentina, *Krapovickas & Cristobal 14675*.
(c) Argentina, *Troncoso et al. 2462*.
(d) Argentina, *Solomon 4131*.
E. nivale. (NIV)
Argentina, *Gentili in 1975*.
E. obscurum. (OBS)
(a) Spain, *Raven 26069*.
(b) Chile, *Ramirez in 1975*.
E. puberulum. (PUBER)
Chile, *Marticorena et al. 1015*.

covered. The first, termed DD, is found in *Epilobium duriaei* Gay ex Godron from Europe (Seavey & Raven, 1977a); the other, termed EE, is found in *E. platystigmatosum* from eastern Asia (Seavey & Raven, 1978). Each of these arrangements differs from the BB by a single reciprocal translocation, and each is different from the AA and CC arrangements. Like the latter two arrangements, DD and EE were probably independently derived from the BB type.

The chromosomal arrangements and some of the crossing relationships within the South American species have now been elucidated. Most of the strains used by Seavey & Raven (1977c), plus a number of additional ones, including several previously uncultivated species, were grown and experimentally hybridized. The hybrid progeny were then examined for chromosomal arrangement and pollen stainability. The strains used in the crossing experiments are given in Table 2, and the results from the hybrids are shown in Tables 3 and 4.

As in previous studies of chromosomal arrangements in *Epilobium*, beginning with those of Seavey & Raven (1977a) and continuing to the present, all of the strains were standardized by crossing them with a single strain of *E. ciliatum*

TABLE 3. Experimental hybrids between species of *Epilobium*. Acronyms and lettered strains refer to Table 2. Female parents are listed first, in alphabetical order, followed by the male parent. Data for voucher numbers below M600 are taken from Seavey and Raven (1977c). All vouchers are deposited at MO; full collection information given under respective species.

Cross	Chromosomal Configuration		Pollen Stainability %	Greenhouse Voucher
AUSTa × CIL	16_{II} + ch4	BB × AA	32	M465
DENTb	16_{II} + r4	BB × AA	45	M435
DENTc	16_{II} + ch4	BB × AA	39	M467
GLAUa	18_{II}	BB × BB	65	M437
WAT	16_{II} + r4	BB × AA	26	M469
AUSTb × DENTc		BB × AA	8	M1542
AUSTc × DENTc		BB × AA	11	M1557
PUBER	16_{II} + r4	BB × AA	38	M1562
BARB × DENTc	16_{II} + r4	BB × AA	12	M1948
GLAUa	18_{II}	BB × BB	69	M1953
CIL × AUSTa	16_{II} + r4	AA × BB	27	M466
BARB	16_{II} + r4	AA × BB	33	M1954
DENTa	18_{II}	AA × AA	37	M455
DENTb	18_{II}	AA × AA	51	M1540
DENTc	18_{II}	AA × AA	56	M1538
GLAUa	16_{II} + ch4	AA × BB	23	M443
WAT	18_{II}	AA × AA	86	M1539
DENSa × GLAUa	18_{II}	BB × BB	88	M441
OBSa	18_{II}	BB × BB	0	M575
DENSb × GLAUa	18_{II}	BB × BB	92	M1552
DENTb × AUSTa	16_{II} + r4	AA × BB	45	M436
CIL	18_{II}	AA × AA	47	M456
DENSa	16_{II} + r4	AA × BB	15	M452
GLAUa	16_{II} + ch4	AA × BB	41	M439
OBSa	16_{II} + r4	AA × BB	33	M459
WAT	18_{II}	AA × AA	24	M457
DENTc × AUSTa	16_{II} + ch4	AA × BB	34	M468
AUSTb		AA × BB	7	M1541
AUSTc	16_{II} + r4	AA × BB	25	M1556
CIL	18_{II}	AA × AA	64, 61	M1537, M1964
BARB		AA × BB	21	M1949
DENSb	16_{II} + r4	AA × BB	27	M1550
GLAUa	16_{II} + ch4	AA × BB	29	M444
OBSb		AA × BB	31, 18	M1561, M1967
GLAUa × AUSTb	18_{II}	BB × BB	84	M1543
AUSTc		BB × BB	97	M1558
CIL	16_{II} + r4	BB × AA	22	M442
DENSb		BB × BB	87	M1551
DENTb	16_{II} + r4	BB × AA	46	M440
DENTc	16_{II} + r4	BB × AA	24	M445
PUBER		BB × AA	44	M1546
GLAUb × AUSTc	18_{II}	BB × BB	83, 68	M1559, M1966
NIV × DENTc	16_{II} + r4	BB × AA	13	M1554
GLAUa	18_{II}	BB × BB	23, 12	M1555, M1965
OBSa × DENSa	18_{II}	BB × BB	0	M576
DENTb	16_{II} + ch4	BB × AA	36	M460
GLAUa	18_{II}	BB × BB	21	M448
PUBER × BARB	16_{II} + r4	AA × BB	56	M1952
GLAUa	16_{II} + r4	AA × BB	47	M1547
WAT × AUSTa	16_{II} + r4	AA × BB	24	M470
DENTb	18_{II}	AA × AA	37	M458

TABLE 4. Experimental hybrids involving *Epilobium hirtigerum*. Acronyms and lettered strains refer to Table 2. Female parents are listed first, in alphabetical order, followed by the male parent. Data for voucher numbers below M600 are taken from Seavey and Raven (1977c). All vouchers are deposited at MO; full collection information given under respective species.

Cross	Chromosomal Configuration		Pollen Stainability %	Greenhouse Voucher
DENTa × HIRTIGb	14_{II} + r4 + ch4	AA × B_1B_1	9	M462
GLAUa × HIRTIGb	16_{II} + r4	BB × B_1B_1	9	M451
HIRTIGa × HIRTIGb	16_{II} + r4	BB × B_1B_1		
HIRTIGb × DENTa	14_{II} + 2 r4	B_1B_1 × AA	14	M463
GLAUa	16_{II} + r4	B_1B_1 × BB	7	M450
HIRTIGc	16_{II} + r4	B_1B_1 × BB	38	M1958
HIRTIGd	16_{II} + r4	B_1B_1 × BB	52	M1955
HIRTIGc × OBSa	18_{II}	BB × BB	64	M1959
HIRTIGd × OBSa	18_{II}	BB × BB	60	M1960
PUBER × HIRTIGc		AA × BB	1	M1961

subsp. *watsonii* (WAT; AA), *E. obscurum* (OBSa; BB), or with another strain that had previously been standardized to the first two.

Only the AA and BB chromosomal arrangements are present in South America. Their distribution among the species is summarized in Table 5. The rationale for the suspected arrangement of the three unknown species is discussed in the section on biogeographical relationships.

Epilobium puberulum is presented as having the AA genome. When this species was crossed with *E. glaucum*, a known BB, the resulting hybrids produced 16 pairs and a ring of four chromosomes at meiotic metaphase I. There is no evidence to suggest that *E. puberulum* has an unusual chromosome arrangement, so it will probably be found to have the AA arrangement. The definitive crosses to known AAs have been made but not yet analyzed.

Epilobium hirtigerum initially presented a perplexing chromosomal situation. The original strain that was tested (HIRTIGb) was found to differ from the BB arrangement by one reciprocal translocation and from the AA by two. The question was posed as to whether this unusual arrangement characterized all populations of *E. hirtigerum* in South America (Seavey & Raven, 1977c). Two additional populations, one (HIRTIGd) from the same general area, and a second from elsewhere in the range (HIRTIGc), were tested against the original strain and a known BB. The results of these crosses are given in Table 4. It now appears likely that the BB arrangement is the normal one for *E. hirtigerum* in South America, as it is in Australasia, and that the original strain tested is atypical.

Plants with anomalous chromosomal arrangements, such as that illustrated by *E. hirtigerum*, are now known in four species. In *E. microphyllum* A. Rich. and *E. palustre* L., single individuals have been found that differed from the BB arrangement by one reciprocal translocation. Other plants of these species from the same or nearby populations, however, had the BB arrangement (Raven, 1972; Seavey & Raven, 1977a). In a similar fashion, a single individual of *E. glaberrimum* Barbey had an arrangement that differed from AA by one reciprocal translocation, but plants from the same and a number of other populations were all

TABLE 5. Distribution of chromosomal arrangements in native South American species of *Epilobium*. See text for further explanation of species marked with asterisk (*).

Species	Arrangement
E. denticulatum	AA
E. puberulum	AA*
E. ciliatum	AA
E. nivale	BB
E. barbeyanum	BB
E. densifolium	BB
E. australe	BB
E. glaucum	BB
E. hirtigerum	BB*
E. pedicellare	Not known, probably AA
E. fragile	Not known, probably AA
E. conjungens	Not known, probably BB

AA (Seavey & Raven, 1977a). It seems clear that these chromosomally differentiated plants probably arose spontaneously within populations. Events of this type provide an example of how the major chromosomal lines might have arisen and how differentiation between species could have proceeded.

Crossing relationships. It has been well established that there are essentially no barriers to the production of viable seed between members of *Epilobium* sect. *Epilobium*, even among geographically and morphologically separated species or between chromosomal groups (e.g., Brockie, 1970; Seavey & Raven, 1977a), although various types of genetic or cytoplasmic incompatibilities may seriously disrupt development or fertility after germination (Thakur, 1965). The failure to set seed in interspecific crosses may occur due to poor pollen tube growth, or failure of fertilization, but these are generally not important factors (Raven & Raven, 1976). The results of this study support this broad conclusion. Seed set may be reduced in artificial crosses, but this is often due to technical difficulties, such as damage to small flowers when they are emasculated, transfer of an inadequate quantity of pollen, or use of pollen from a short-styled species to cross with a long-styled one. In all cases, at least some seed was produced in interspecific crosses.

The hybrids that were made with the South American species, with few exceptions, showed no developmental abnormalities or reciprocal differences such as those that have been reported by Thakur (1965), Michaelis (1954, 1965), and Raven & Raven (1976). Hybrids between *E. obscurum*, a European species, and *E. densifolium*, *E. glaucum*, and *E. australe* were all initially dwarf. Only one plant of the hybrid combination *E. obscurum* × *E. glaucum* eventually flowered vigorously. The other combinations either died or flowered only sporadically (Seavey & Raven, 1977c). Similarily, hybrids between *E. denticulatum* and *E. obscurum* were also initially dwarf, and only two individuals eventually produced normal branches and flowered. These hybrids, which involved both the AA and BB chromosomal groups (Table 5), would strongly suggest some type of genetic or cytoplasmic incompatibility specifically with *E. obscurum*, although its precise nature is not known. The hybrid between *E. nivale* and *E. glaucum* may also

have been disturbed developmentally. Although the plants were vigorous vegetatively, they produced very few flowers. Alternatively, this could be the result of the relatively low number of flowers that *E. nivale* normally produces under greenhouse conditions.

In the absence of obvious developmental barriers to hybridization, one must utilize other data to assess the degree of relationship between species. Besides the chromosomal arrangements that divide the South American species into two groups, hybrid fertility, as indexed by the percentage of stainable pollen (Table 6), can also be used as a measure of relationship. This data must be used cautiously, however, because pollen stainability can vary considerably from plant to plant and even between flowers on the same plant, and it is often greatly affected by the age of the plant and the cultural conditions under which the plant has been grown.

The pollen fertility of most non-hybrid plants used in the experimental hybridizations was greater than 85%, with two exceptions, *Epilobium denticulatum* (DENTc), which had 75%, and *E. barbeyanum* (BARB), which had 54%. Even crosses made between strains of the same species from widely separated geographical areas had high fertility (e.g., *E. denticulatum*: *Averett 1004*, Peru × *Billings 161*, Venezuela, 94%; *E. ciliatum* subsp. *ciliatum*, *Zöllner 7868*, Chile × *E. ciliatum* subsp. *watsonii*, *Sharp in 1967*, California, 86%).

The much reduced pollen fertility seen in Table 6 between species with different chromosomal arrangements is due primarily to the high frequency of adjacent disjunction of the chromosomes involved in the ring of four during meiosis. The consequent duplications and deletions resulted in a substantial number of aborted gametes (Seavey, 1977). Hybrids between species with the same chromosomal arrangement that show reduced fertility must have other factors involved.

Epilobium ciliatum and *E. denticulatum*, both with the AA arrangement, have differentiated genetically and produce hybrids with substantially reduced fertility. Within the group of species with the BB arrangement, *E. glaucum* when crossed with *E. australe* or *E. densifolium* produces hybrids with variable, but sometimes very high, fertility, up to 97% and 92% respectively (Table 6). These values are similar to those reported for hybrids between many closely related species in Australasia (Raven & Raven, 1976). This suggests that these three species are fairly closely related to one another, although they are morphologically distinct. The relationship of *E. barbeyanum* to these species is still obscure. *Epilobium nivale*, on the other hand, is quite strongly differentiated from *E. glaucum*, either genetically or cytoplasmically, as indicated by the very low hybrid pollen stainability and the disturbed development mentioned earlier. Its relationship with the other species remains unknown.

Biogeographical Relationships

The morphological and cytological evidence presented previously suggests that there have been a minimum of five pre-European introductions of *Epilobium* into South America with subsequent diversification in some of these lines. The probable source of progenitors for each group and the relationships of the cur-

TABLE 6. Percent of stainable pollen in experimental hybrids of *Epilobium*. Acronyms refer to Table 3.

		AA			BB						STANDARDS	
	♂/♀	DENT	PUBER	CIL	NIV	BARB	DENS	AUST	GLAU	HIRTIG	OBS	WAT
AA	DENT	·	·	47, 61, 65	·	21	15, 27	7, 25, 34, 45	29, 41	·	18, 31 33	24
	PUBER	·	·	·	·	56	·	·	47	1	·	·
	CIL	37, 51, 56	·	·	·	33	·	27	23	·	·	86
BB	NIV	13	·	·	·	·	·	·	12, 23	·	·	·
	BARB	12	·	·	·	·	·	·	69	·	·	·
	DENS	·	·	·	·	·	·	·	88, 92	·	0	·
	AUST	8, 11, 39, 45	39	32, 34	·	·	·	·	65, 76	·	·	26
	GLAU	24, 46	44	22	·	·	87	68, 83, 84, 97	·	·	·	·
	HIRTIG	·	·	·	·	·	·	·	·	·	64, 60	·
STANDARDS	OBS	36	·	·	·	·	0	·	21	·	·	·
	WAT	37	·	·	·	·	·	24	·	·	·	·

TABLE 7. Distribution and probable sources of progenitors for related groups of native species of *Epilobium* in South America. AA and BB refer to chromosomal arrangements; see text for further discussion.

Group/Species	Distribution	Source of Progenitor
Group I (AA)		North America
E. denticulatum	Andes, Venezuela to northern Argentina and Chile; Costa Rica	
E. fragile	Altiplano of Peru and Bolivia	
E. pedicellare	Altiplano of Peru and Bolivia	
E. puberulum	Central Chile	
Group II (AA)		North America
E. ciliatum	Southern Andes of Chile and Argentina, Falkland Islands; widespread in North America	
Group III (BB)		Australasia
E. australe		
E. barbeyanum	Southern Andes of Chile and Argentina	
E. densifolium		
E. glaucum		
E. nivale		
Group IV (BB)		Australasia
E. hirtigerum	Eastern Argentina, Uruguay and southern Brazil; widespread in Australasia	
Group V (BB)		Australasia
E. conjungens	Tierra del Fuego and adjacent islands	

rently recognized species are summarized in Table 7 and discussed in detail below.

The two groups with the AA chromosomal arrangement almost certainly have ancestral affinities with North America. These are the only species with the AA arrangement in the Southern Hemisphere. The other species with this arrangement are found primarily in North America, with only three isolated species in western Europe.

Epilobium denticulatum is the most widespread and variable species of the first group in Table 7, and highly characteristic of the páramos and puna throughout the northern and central Andes. Although *E. pedicellare* and *E. fragile* are unknown chromosomally, they appear to be closely allied to *E. denticulatum* on morphological grounds, and will probably be found to have the AA chromosomal arrangement. *Epilobium pedicellare* shares with *E. denticulatum* the feature of appressed, blunt-tipped hairs on the leaf surfaces, a similar habit, and completely overlapping geographical ranges. The relationships of *E. fragile* are somewhat more problematical because of its reduced stature and restriction to extremely high elevations, but it is probably closely related to and may be directly derived from *E. denticulatum*. The geographical range of *E. fragile* is also completely contained in that of *E. denticulatum*, and some small specimens of *E. denticulatum* approach *E. fragile* in overall morphology. Certainly this might be the result of convergence, but no alternative placement for *E. fragile* is apparent. These three species are the only ones found in the northern and central Andes; all of

the others are restricted to areas mostly south of 30°S latitude. *Epilobium puberulum*, although isolated geographically in central Chile from the species discussed above, is morphologically similar to some populations of *E. denticulatum* and has often been confused with that species.

The precise relationships between these four species is not clear, and none of them resemble any extant North American species, but North America is the only reasonable source for progenitors, which probably arrived in South America by long-distance dispersal. The ancestor of these species was probably an early offshoot of the AA chromosomal line that gave rise to the members of the *E. ciliatum* complex in North America (Hoch, 1978).

The second AA chromosomal group consists only of *Epilobium ciliatum* subsp. *ciliatum*. The South American populations, which are found in areas south of 30°S, have gone under various names, most often *E. chilense*, *E. valdiviense*, or *E. magellanicum*. Only recently has the question been raised as to whether populations from South America were closely related to ones from North America (Seavey et al., 1977; Seavey & Raven, 1977c), although some South American plants had been identified as North American species and vice versa many years ago (Haussknecht, 1879, 1884).

In 1977, Seavey et al. discovered that the seed surface morphology of plants identified as *Epilobium chilense* were identical with those found in *E. ciliatum* in North America. As was discussed earlier, this seed type is restricted to two species in North America. In addition, these South American plants produced turions or leafy rosettes, overwintering structures that are unique in South America but are common in a number of species in North America. An analysis of the *E. ciliatum* complex in North America by Hoch (1978) provided additional morphological features as a basis for comparison. In this study he recognized five species, including *E. glaberrimum* Barbey with two subspecies and *E. ciliatum* with three subspecies. A careful comparison of plants from many widely separated South American populations with others from North America indicated that there were few differences between them and that all the South American populations could easily be accommodated in *E. ciliatum* subsp. *ciliatum* as circumscribed by Hoch. In fact, the variability seen in South America is only a part of that exhibited by this subspecies in North America, where it is extremely diverse and widespread. *Epilobium ciliatum* in South America has been derived from North America and may have originated from a single introduction.

There is an unlikely possibility that *Epilobium ciliatum* arrived in South America as an unintentional introduction by man. Beginning in the 1760s, with the founding of a number of missions in Alta California, increased commerce began between the western coast of North America and Peru and Chile. Prior to this time, only rare and casual visits had been made to North American areas where *E. ciliatum* occurs. Thus, the most likely time of introduction would have been after this date. The first South American collections of *E. ciliatum* were made about 1793 in central Chile, and by 1833 in Tierra del Fuego, a period of only 40 years. Considering the extensive variation and presence of *E. ciliatum* in many areas that were remote from human habitation over a geographic distance of 2,700 km in South America, it seems unlikely that *E. ciliatum* has been introduced within the past 200 to 300 years. Rather, its occurrence in South America is

probably the result of a pre-European long distance dispersal event (cf. Raven, 1963).

The species with the BB chromosomal arrangement, however, probably have their affinities with Australasian species. They have been divided on the basis of morphology into three groups, one with five species, the other two with one each, representing three independent introductions (Table 7).

Epilobium australe, *E. barbeyanum*, *E. densifolium*, and *E. glaucum* are fairly closely related, with *E. nivale* being somewhat anomalous, but also probably allied. These species are morphologically unlike any North American species with the BB chromosomal arrangement, but they also show no obvious affinities with any extant species in Australasia. The habit, simple leafy shoots as perennating structures, and the rather broadly obovoid seeds (cf. Raven & Raven, 1976) suggest an Australasian relationship.

Epilobium hirtigerum is conspecific with a widespread species of Australia and New Zealand. For many years the South American populations were called *E. brasiliense*. However, during the intensive study that led to their monograph of *Epilobium* in Australasia, Raven & Raven (1976) discovered that the South American plants were indistinguishable from those found in many populations in Australasia, especially New Zealand. The examination of a large sample of specimens from South America for the present study confirms this conclusion. Philibert Commerson made collections of this species in Uruguay two years prior to the first known European landings in eastern Australia or New Zealand by Captain James Cook in 1769. Unless some unknown, fortuitous historical event aided introduction of this species, it seems highly probable that *E. hirtigerum* arrived in South America by long-distance dispersal. It also seems likely that the present populations were derived from a single introduction from Australasia.

The third group contains only *Epilobium conjungens*. This species has what can be considered the most unusual morphology of any South American species. The stems are prostrate, growing and rooting beyond the flowers, producing small mats, with the flowers scattered singly, often widely, along the stem, and with consistently opposite leaves. This combination of features is shared with 13 species restricted to Australasia and no others. In describing *E. conjungens*, Skottsberg (1906) drew attention to its apparent close relationship to the creeping species of Australasia and placed it nearest to *E. nummulariifolium* A. Cunn. and *E. brunnescens* (Cockayne) Raven & Engelhorn (as *E. pedunculare* A. Cunn.), based on Haussknecht's *Monographie* (1884). He considered it "ein weiteres Bindeglied," a wide (distant) connecting link between the floras of Tierra del Fuego, where *E. conjungens* is endemic, and New Zealand. The epithet "conjungens," chosen by Skottsberg, reflects this relationship, meaning connected or united, and referring to its floristic affinities.

More recently, the distinctive habit of *Epilobium conjungens* was interpreted to be the result of convergent evolution, since it was believed that *E. conjungens* had a few flowered, terminal inflorescence (Raven & Raven, 1976). An examination of material unavailable to them, however, shows clearly that *E. conjungens* possesses all the features that are unique to the creeping Australasian species. In addition, the flowers of *E. conjungens* are white as they are in all other creeping species. It seems certain that *E. conjungens* was derived from an Australasian

progenitor. Although the chromosomal arrangement of *E. conjungens* is not known, the presence of only the BB type in Australasia suggests that *E. conjungens* will be found to have that arrangement also.

Ancestors of these three groups probably arrived by long-distance dispersal via the prevailing westerlies. These winds blow continuously, between 30° and 60°S latitude, and are four times as strong as their Northern Hemisphere counterparts (Lamb, 1959). They have undoubtedly played an important role in the dispersal of organisms between southern land masses (Raven, 1973a). *Epilobium* seeds are highly dispersable by wind. Each seed has a coma of long silky hairs at the chalazal end. Once the capsule has dehisced, the seeds can be moved many meters by even light breezes.

A striking representation of the capacity of the Southern Hemisphere westerly winds to affect movement between Australasia and southern South America is illustrated by a recent balloon experiment (Mason, 1971). A radio controlled balloon was released from Christchurch, New Zealand, held at about 12,000 m, and followed by satellite. During the 102 days of tracking, it made eight circuits of the globe, and repeatedly crossed south Australia, New Zealand, southern South America, and southern Africa. On most circuits it required only four to six days to traverse the distance between New Zealand and South America. Of special interest in connection with this pattern of dispersal is the presence of 13 species of *Epilobium* in the Chatham Islands, 800 km east of New Zealand. Equally suggestive of an initial origin in Australasia for the three groups of species with the BB chromosomal arrangement now found in South America is that all of them are restricted to areas south of 30°S latitude, precisely in the path of the prevailing winds. With their high fecundity and persistent autogamy, the introduction of a single *Epilobium* seed in a suitable habitat would provide the basis for a founding population.

The foregoing discussion clearly shows the diverse origins of *Epilobium* in South America and provides examples of two major types of temperate disjuncts found in the New World, amphitropical and circumaustral (Moore, 1972; Raven, 1963, 1973b), both at the individual species level and at higher species groupings. The data available for *Epilobium* reinforces the conclusions of the papers just cited, that most disjuncts in common between North and South America have been derived by dispersal from north to south, and those between Australasia and South America from west to east.

EVOLUTIONARY HISTORY

The time of arrival and the impact of geological events on the various groups of *Epilobium* in South America is important to an understanding of their evolutionary history. In the absence of any fossil data on *Epilobium* in South America, except in a few apparently recent (late Pleistocene) but poorly dated pollen samples from Patagonia and Tierra del Fuego (Auer, 1958), the evidence for the time of appearance of *Epilobium* in South America is dependent on information about the availability of suitable habitats and on the presence of *Epilobium* in the presumed source areas.

As was discussed earlier, the genus *Epilobium,* based on its current distribution, possibly evolved in western North America and spread from there throughout the Northern Hemisphere, entering the three Southern Hemisphere continents only secondarily. In Australasia, *Epilobium* apparently did not arrive from Asia until the late Pliocene (Raven, 1973a; Raven & Raven, 1976). Prior to this time, from the Cretaceous to the mid-Miocene, Australasia was much further south than it is at the present and was separated initially by a gap of at least 3,000 km from points in southeast Asia (Raven, 1979b). During this period, Australasia was dominated by temperate forests (Raven, 1973a), while southern Asia was tropical, with low relief (Raven, 1979b), and hence, an area unlikely to have had *Epilobium* at that time. It was only during the late Pliocene, after Australasia had moved sufficiently far northward to encounter the Asian Plate, that mountains with cool-temperate climates were formed in Malaysia, Sumatra, Luzon, and New Guinea that could serve as intermediate points for the long-distance migration of temperate Asian species into Australasia. The earliest records of *Epilobium* in New Zealand are from the late Pliocene (Raven & Raven, 1976). Thus, Australasia could not have served as a source area for *Epilobium* in South America until at least the late Pliocene, and probably later.

North and South America were widely separated until the Eocene, at which time South America was more or less equidistant from Africa and North America. From that point on, they moved closer to one another and gradually underwent orogenies that eventually resulted in a land connection about 3.1 million years ago (Keigwin, 1978; Marshall et al., 1979). Suitable temperate habitats for *Epilobium,* however, did not occur in South America throughout that time, except perhaps in the far South where *Nothofagus* forests similar to those in Australasia existed (Simpson, 1973; Vuilleumier, 1969).

A review of palynological and geological studies suggests that the Andes are a very recently evolved mountain range that did not attain high elevations until the late Pliocene or even the early Pleistocene (Flenley, 1979; Hammen, 1974, 1979; Simpson, 1975, 1979). The present-day Andes are composed of a rather large number of structural-tectonic units that have undergone separate orogenies involving uplift, folding, faulting, and vulcanism, but resulting in a more or less concurrent elevation of the entire range.

At the end of the Cretaceous most of the land that now forms the Andes had been elevated above sea level and gradual uplifting continued until the Miocene. During this time, elevations in excess of 1,000 m were probably infrequent, at least in the north (Hammen, 1979). Throughout most of this period the Andean region was covered with tropical forests that extended much farther south than at present and merged gradually with subtropical and temperate forest elements in the far south (Cei, 1979).

Beginning in the Miocene and continuing into the Pliocene increased vulcanism and crustal movements uplifted the mountains even more, but it is doubtful if there were significant areas of elevation over 2,000 m (Simpson, 1979).

During this same period, the initial phases of climatic deterioration in southern South America began, which ultimately culminated in the glacial events of the Pleistocene. The major trend was toward a cooler, drier climate, with increasing

rain shadow effects from the rising Andes, which resulted in the breakup of Patagonian forest lands and the migration of more mesic tropical and subtropical elements northward (Báez & Scillato, 1979).

The middle and late Pliocene saw a major increase in orogenic activity that continued into the Pleistocene and resulted in an average uplift of 1,000 to 3,000 m throughout the Andes. Thus, all of the floristic elements that are currently found at high elevations must have been derived during the past two to five million years, either by migration from other temperate areas or by vertical evolution from pre-existing lowland tropical elements (cf. Cleef, 1979).

The first indication of open páramo-like habitats is found in the northern Andes in upper Pliocene formations and consists of a high representation of Gramineae, Compositae, and *Hypericum* (Hammen, 1979). All the species of *Epilobium* of apparently North American extraction (AA), except *E. ciliatum* and *E. puberulum*, occur in the páramo and puna north of central Chile and Argentina. It is unlikely that the North American progenitor of these species could have arrived and become established prior to the late Pliocene, and it may have appeared even later.

Species such as *E. ciliatum* and *E. hirtigerum* probably arrived during or after the last glaciation. The ancestor of *E. conjungens* almost certainly arrived after the last glacial advance, since Tierra del Fuego and adjacent islands, where it is endemic, were completely ice-covered at that time (Vuilleumier, 1971).

Climatic deterioration in the late Tertiary finally resulted in the drastic fluctuations between glacial and interglacial climates that characterized the Pleistocene. Tropical regions were significantly affected by alternating climates just as were more temperate areas.

In the tropical Andes, there is evidence for one to four glaciations that, during the last glacial advance, resulted in the lowering of tree line from 1,200–1,500 m below its present level, and a reduction of mean temperature by 6–7°C, at least in the Andes of Colombia (Hammen, 1974). Glacial periods were colder and drier than interglacials, resulting in the downward movement of vegetation zones, generally with an increase in their areal extent, and expansion of some xeric vegetation types at the expense of moist or wet tropical ones, especially in the lowlands (Haffer, 1979). The impact of actual glacial ice during these periods was not as great in the tropics as the heavy glaciation in more temperate latitudes; although substantial glaciation took place in the cordilleras of Peru and Bolivia and on other high mountains elsewhere (Vuilleumier, 1971). During interglacials, the climate was warmer and probably wetter, resulting in an upward movement of vegetational zones, contraction of páramo vegetation and an expansion of more mesic forest types. For páramo and dry lowland floras, the interglacials were a time of isolation and differentiation, and vice versa during glacials.

In temperate South America, the impact of glacial events was in many ways much more severe than in the tropics. There is abundant evidence for four glaciations that covered large areas of the southern Andes with glacial ice. Between 30°S and 44°S there were extensive montane glaciers extending to progressively lower elevations. Some of these produced major ice barriers in a number of river valleys in central Chile (Simpson, 1979). From about 44°S latitude the entire Andes chain was covered with glacial ice to sea level on the western slope and

to the base of the mountains on the east. The area covered by ice included all of Tierra del Fuego and the southern tip of Patagonia (Vuilleumier, 1971). Glacial advances effectively lowered vegetation zones in temperate South America, which allowed alpine and other high elevation vegetation to cover more extensive, continuous areas and produce regions of secondary contact between formerly isolated populations. At the same time, it caused contraction and shifting of *Nothofagus* forest regions northward (Simpson, 1973). During interglacials these same alpine vegetation types were isolated in upper montane areas where they could undergo independent differentiation.

The effects of Pleistocene climatic fluctuations on speciation patterns in *Epilobium* are not at all clear, and may have had relatively little impact, unlike patterns found in other Andean groups that have apparently diversified greatly under alternate contraction and expansion of ranges (e.g., *Perezia multiflora* complex, Simpson, 1973; *Arracacia*, *Lleracia*, Simpson, 1975). Of the tropical species, only *E. denticulatum* shows extensive morphological diversity through its large range in the páramo and puna. Interestingly enough, *E. denticulatum* achieves its greatest variability in the altiplano and cordilleras of Peru and Bolivia, with diminishing diversity both north and south of there. This area is the part of the range of *E. denticulatum* that was most heavily glaciated during the Pleistocene, so glacial advances and retreats may have influenced the variation patterns now seen. The high dispersability of *Epilobium* seed, however, may exclude glaciers from acting as actual barriers. Alternatively, this great diversity may be due to the large number of habitats at various elevations available for colonization by *E. denticulatum* in this region.

Unlike *Epilobium* in New Zealand, which has undergone an explosive radiation of many closely related species adapted to a diverse array of habitats through hybridization and persistent autogamy, the largest group of closely related species in South America contains only five members (*E. australe*, *E. barbeyanum*, *E. densifolium*, *E. glaucum*, and *E. nivale*). Each of these is very distinctive, with mostly overlapping ranges, and no one of them can be said to have been derived by hybridization between any other two species. These species may have evolved under the isolation-habitat specialization model suggested above, but at the present time interpretation of their inter-relationships remains perplexing and awaits new insight.

Pleistocene glacial advances also affected the current geographical distribution of some of the species. All of the species except three are found almost exclusively south of 30°S. Between the latitudes of 27°S and 31°S there was a band of persistent aridity that crossed the Andes and was an effective barrier during both glacial and interglacial periods (Simpson, 1979). *Epilobium ciliatum*, *E. glaucum*, and *E. barbeyanum* all reach their northern limits at the southern edge of this zone. Only *E. denticulatum* has managed to cross this barrier in a narrow strip along the eastern slope of the Andes, south to about 34°S. In southern South America, the heavy glaciation south of 44°S, eliminated much of the montane vegetation. There are a large number of species that reach their southern limit at about this latitude (Simpson, 1973), including *E. barbeyanum* and *E. densifolium*, which are not known from south of about 42°S.

One of the more peculiar distributions seen in *Epilobium* is that of *E. nivale*.

It too reaches the southern limit of its primary range at about 42°S, but then reappears in the vicinity of Lago Argentino (51°S), indicating a gap in its range of about 800 km. Other species, such as *Isoetes savatieri* Franch. (Donat, 1931), the species pair *Perezia bellidifolia* (Phil.) Reiche and *P. megalantha* Speg. (Simpson, 1973), and *Gunnera tinctoria* (Mol.) Mirbel (Pisano, pers. comm.), have similar distributions, which has led some authors (Auer, 1958; Skottsberg, 1916; Donat, 1931; Simpson, 1973) to suggest that there was a refugial area to the east of the Andes in the far south where these and other species managed to survive during the heaviest glaciations, while they were eliminated in between. It is possible that *E. nivale* does occur in the intervening area because the Patagonian Andes have been little explored botanically, and *E. nivale* inhabits high, relatively inaccessible areas near the snow line.

REPRODUCTIVE BIOLOGY AND HYBRIDIZATION

Breeding system. The majority of the species of *Epilobium* sect. *Epilobium* are autogamous, with only approximately 10% of the 170 species modally outcrossing. All are self-compatible, and, in those that are capable of self-fertilization, a full complement of seed is normally produced.

Epilobium species in South America possess a diversity of breeding systems, from modally outcrossing to cleistogamous, but all of them can produce seed by self-fertilization (see review in Raven, 1979a). Nearly all the species have pale pink to rose purple flowers, including the three introduced species. Only *E. hirtigerum, E. denticulatum, E. ciliatum,* and *E. conjungens* have petals that are white or vary from white to pink. Flower color appears to be significantly related to the degree of outcrossing, as pointed out by Raven & Raven (1976), since insects are more likely to visit the colored flowers than white ones.

Epilobium densifolium has the largest number of features typical for a modally outcrossing species. The flowers are large (petals up to 1.2 cm long), with the anthers held away from the stigma at anthesis, and usually the stigma partially exserted. Each flower produces a large droplet of nectar. *Epilobium australe, E. glaucum,* and *E. barbeyanum* have smaller flowers, but in them also, the anthers are held away from the stigma at anthesis. In these four species, usually after a period of several hours, the longest stamens gradually bend inward and the dehisced anthers make contact with the receptive stigma. Nonetheless, they are all modally outcrossing.

Epilobium denticulatum has separate or even mixed populations of large- and small-flowered plants. In this species, the large flowers also have the anthers separated from the stigma, at least for a few hours. The balance of the species, including the small-flowered populations of *E. denticulatum,* have flowers that are more or less immediately self-pollinated at anthesis. Functional cleistogamy seems to be the general condition for *E. hirtigerum,* where the anthers may dehisce prior to the opening of the flower bud. Generally, the anthers dehisce at anthesis, although there may be up to a few hours delay. In addition, all species, except *E. hirtigerum* and some plants of *E. ciliatum,* produce at least a small amount of nectar that may be attractive to flower visitors.

Weather conditions have a very strong effect on the extent to which the

flowers of *Epilobium* open at anthesis. All species open their flowers fully on bright sunny days, including *E. hirtigerum*. On cloudy or rainy days, however, most plants open their flowers only partially or not at all, very strongly reducing the chances of cross-pollination or eliminating that possibility completely by being functionally cleistogamous.

Despite the various features that might promote some outcrossing, insect visitation to any of the species appears to be quite rare. In many hours of observation, at all times of the day and under various weather conditions, only two insect visitors were observed. Several unidentified medium-sized syrphid flies were seen visiting flowers of *Epilobium barbeyanum* in a large streamside bog near Lagunillas, Cordillera Prov. (Santiago), Chile; and a single visit by a small, unidentified bee to several plants of *E. denticulatum* with medium-sized flowers in a population near Rinconada, Dpto. La Paz, Bolivia was observed.

Even though a number of species have floral morphologies suggestive of outcrossing, it is clear that there remains a high degree of autogamy in most species. Autogamy is probably the primary means by which populations maintain their distinctness from one another, and it is certainly a strong force in limiting interspecific hybridization. Persistent autogamy does not prevent outcrossing, it merely reduces the frequency of an outcrossing event taking place. While cleistogamy may be the functional mode of pollination in some populations or species, occasional intra- and interspecific crosses between many of these species do occur, providing new genetic variability for segregation and recombination. Even crosses between groups that have developed some internal barriers to hybridization produce occasional fertile seeds that may be capable of surviving. In essence, then, every population is under its own selective pressure, to which it adjusts by reproducing well adapted genotypes and occasionally, through outcrossing, obtains new genetic material.

Ecological relationships. Many South American species of *Epilobium* grow in habitats similar to those in which species in other parts of the world are found; that is, in moist, often disturbed, open sites such as stream banks, ditches, seeps, bogs, lakeshores, etc. Other South American species exhibit a striking amount of ecological specialization, however, which further isolates a number of distinct species. The following list provides a synopsis of the ecological preferences of the various species: *E. australe,* almost always in or near running water, broad elevational range; *E. barbeyanum,* alpine bogs and very wet sites, stems often floating; *E. ciliatum,* any moist, disturbed site, broad elevational range; *E. conjungens,* moist moss mats above timberline; *E. densifolium,* stabilized alpine scree, often away from water, but also along rocky stream banks; *E. denticulatum,* any moist site, broad elevational range; *E. fragile,* moist cracks and crevices in rocks, above 4,500 m; *E. glaucum,* almost always in or near running water, broad elevational range; *E. hirtigerum,* marshes, wet places, mostly at low elevations; *E. nivale,* alpine, along rivulets and other permanently wet spots, up to permanent snow line; *E. pedicellare,* steep or vertical seeps, altiplano; *E. puberulum,* moist disturbed places, mostly at low elevations.

Sympatry. Despite rather strong ecological differences and geographical separations, many species do occur sympatrically, at least in part of their range.

TABLE 8. Sympatric occurrence of native species of *Epilobium* in South America. Acronyms are those given in Table 2. In addition, PED = *E. pedicellare*, FRAG = *E. fragile*, and CONJ = *E. conjungens*. KEY: * = species that occur together and hybridize; + = species that occur together; ? = species that probably occur together.

DENT	·											
PED	*	·										
FRAG	?	·	·									
PUBER	·	·	·	·								
CIL	*	·	·	*	·							
NIV	·	·	·	·	+	·						
BARB	·	·	·	·	*	?	·					
DENS	·	·	·	·	+	+	?	·				
AUST	·	·	·	·	*	+	+	*	·			
GLAU	+	·	·	+	*	+	*	*	*	·		
CONJ	·	·	·	·	·	·	·	·	?	·	·	
HIRTIG	+	·	·	·	*	·	·	·	·	·	·	·
	DENT	PED	FRAG	PUBER	CIL	NIV	BARB	DENS	AUST	GLAU	CONJ	HIRTIG

This is especially true in the Andes of central Chile and Argentina at moderate elevation (1,000–1,500 m), where two or more species are often found very near each other, if not intermixed. Up to five species have been seen growing together near the Termas del Río Blanco, Malleco Prov., Chile, at 1,300 m; namely *Epilobium australe*, *E. ciliatum*, *E. densifolium*, *E. glaucum*, and *E. nivale*.

Table 8 summarizes the sympatric occurrence of the native species in South America. The information was obtained primarily from personal observation and mixed herbarium collections, or rarely deduced from locality information. There are a number of combinations that cannot occur because the ranges of the species involved do not overlap. Likewise, there are several sympatric combinations that should occur, but which have not been seen. These are also indicated in Table 8. One of the introduced species, *Epilobium obscurum*, has been found growing mixed with *E. puberulum* and *E. ciliatum*, and is known to hybridize with the latter.

Natural hybridization. The occurrence of natural hybrids has been commented on for many years, beginning with Haussknecht (1884), although the frequency with which they are recognized depends greatly on how finely the species delimitations are drawn. Natural hybrids in *Epilobium* are found throughout the world, although constraints are imposed on their formation by a high degree of autogamy or internal barriers to hybridization.

Very few hybrids have ever been reported from South America, primarily because of the lack of material and field examinations. Samuelsson (1923, 1930) reported hybrids between *E. denticulatum* and *E. hirtum*, now considered to be conspecific, and between *E. denticulatum* and *E. haenkeanum* (= *E. pedicellare*). Only one specimen of the latter combination is now considered to be of hybrid origin, although hybrids between *E. denticulatum* and *E. pedicellare* are difficult to distinguish.

Eleven combinations that are known to form natural hybrids are indicated in Table 8 and documented by specimens whose pollen fertility and seed set have been estimated. These are discussed in detail under the individual species treat-

ments. The majority of natural hybrids have morphology intermediate between the two parents and are often characterized by reduced pollen stainability and seed set. A number of hybrid combinations would be difficult to detect, e.g., *Epilobium australe* × *E. nivale* or *E. australe* × *E. densifolium*.

Wherever two or more species occur together hybrids can be formed, but they are relatively infrequent. This, in part, may be due to the ecological distinctness of the habitats in which some species grow, or to other types of barriers to the successful production of hybrid individuals. In contrast to the situation in New Zealand (Raven & Raven, 1976) where hybridization is seen as a central force in the formation of new adaptive genotypes, the South American species, because of their heterogeneous origins, and perhaps the recency of their arrival, have diversified to only a small extent, and not primarily through hybridization.

Taxonomic History

The first botanist to acquire specimens of *Epilobium* from South America was Philibert Commerson, who found *E. hirtigerum* growing near Montevideo, Uruguay, in 1767 when the survey ships *Etiole* and *Boudeuse,* under the command of Louis de Bougainville, stopped on their voyage to the western Pacific. Unfortunately, Commerson died in Mauritius in 1773, before he had a chance to study his collections critically. These were then forwarded to France and incorporated in the collection of the Jardin du Roi.

At this same time, Captain James Cook was also exploring southern South America and the Pacific. With him on his first voyage were the celebrated Joseph Banks and Daniel Solander. Among their many new collections was a second species, *Epilobium australe,* from Tierra del Fuego, collected in 1769.

Somewhat later in the eighteenth century, two major scientific expeditions were financed by the government of Spain, the renowned travels of Hipolito Ruiz, José Pavón, and Joseph Dombey to Peru and Chile (1778–1788), and the Malaspina Expedition, which was sent to survey Spanish territories in the Pacific (1789–1794). During the extensive peregrinations of the former, species of *Epilobium* were encountered in several places, such as Chancay and Tarma, Peru, and Concepción, Chile. The specimens from Peru represented *E. denticulatum,* and those from Concepción were a fourth species, *E. puberulum.* All of these collections, however, were published as *E. denticulatum,* the first name of any South American species to find its way into print (Ruiz & Pavón, 1802).

The Malaspina Expedition was fortunate in having the services of two well trained botanists, Luis Née and Thaddeus Haenke. They prepared many thousands of specimens from South America, Mexico, North America, and the western Pacific. Among these were *Epilobium pedicellare* from Peru collected by Haenke and *E. ciliatum, E. glaucum,* and *E. barbeyanum* from Chile, collected by Née. The latter species were most likely acquired when Née left the expedition at Concepción in late 1793 to go overland via Santiago, crossing the Andes to Mendoza and thence across the pampas to Buenos Aires. There, in May 1794, he rejoined the expedition with nearly 10,000 specimens for the return to Spain (Safford, 1905). Unfortunate political circumstances intervened, so that most of the results of the expedition were never published. A set of Haenke's material was sent to Karl Presl in Prague, who later published *E. pedicellare* along with

many other species in his *Reliquiae Haenkeanae* (Presl, 1831). Née's voluminous collections went to the Royal Botanic Garden in Madrid where some plants were eventually described and published, but the majority were not. Thus, by the end of the eighteenth century, eight of the twelve native taxa recognized in this treatment had been collected, but the first name for any of them was not published until 1802.

The time between 1820 and 1870 saw an increasing number of coastal surveys and penetrations of the interior, especially in southern South America. Most notable among the naval surveys were the United States Exploring Expedition under the command of Charles Wilkes (1838–1842), the Antarctic Expedition of James Ross (1839–1842) with J. D. Hooker as botanist, the first voyage of the *Adventure* and *Beagle* under the command of Philip King (1826–1830), and the second voyage of the *Beagle* commanded by Robert FitzRoy, with Charles Darwin as naturalist (1831–1836). At the same time, a substantial number of botanists were spending extended periods of time in limited areas throughout the continent. Those who are especially important to the chronology of South American *Epilobium* were the collecting forays of E. Poeppig, T. Bridges, H. Cuming, C. Gay, and R. Spruce.

During this period of active exploration, there was still a great deal of confusion about the limits of the species. It is not surprising, when one considers the variability of many *Epilobium* species, that the new South American plants could be equated with variable European species (e.g., *E. nivale* with *E. alpinum*, *E. ciliatum* with *E. tetragonum*). J. D. Hooker was quite perplexed by the species of *Epilobium* from the Andes, and considered most of them to be variants of *E. tetragonum*, one of which he felt was sufficiently distinct to be described as a new variety, *E. tetragonum β antarcticum* (= *E. australe*) (Hooker, 1847, 1853). Quite frequently South American plants were rather arbitrarily given one of three names, *E. denticulatum*, *E. tetragonum*, or *E. pedicellare*. This state of affairs persisted even to the beginning of the twentieth century, when *E. tetragonum* was still being reported as the name for several different species (Macloskie, 1905; Arechavaleta, 1902).

Carl Haussknecht, beginning with a series of papers in 1879 and culminating in his *Monographie der Gattung Epilobium* in 1884, published many new taxa. He had the advantage of studying the collections of many of the major herbaria of Europe, and thus had more South American material at his disposal than any previous author. Perhaps equally as important was his worldwide familiarity with the genus. He was able to dispel the notion that common European species occurred in southern South America, and he recognized several common taxa as separate species for the first time, e.g., *Epilobium chilense* (= *E. ciliatum*) and *E. australe*. Haussknecht was rather confused by the taxa allied to *E. denticulatum*, but such was the authority of his work that some of his errors were perpetuated, resulting in the report of names such as *E. bonplandianum* and *E. caesium* from central Chile (Reiche, 1898). In total, Haussknecht recognized 18 taxa, representing 9 of the 12 native species presented in this treatment.

Among the most important collections used by Haussknecht in the preparation of the *Monographie* were those of Eduard Poeppig and Rudolfo Philippi. Poeppig made extensive collections in central Chile from 1827 to 1829; R. A. Philippi

arrived there in 1851 with his son Federico, both of whom worked intensively on the flora of Chile for more than 50 years.

Subsequent to Haussknecht's work, R. A. Philippi described seven new species of *Epilobium* (Philippi, 1893) that are here considered conspecific with previously described taxa. Further botanical explorations in Chile and Patagonia during the early years of the twentieth century, especially by Per Dusén and Carl Skottsberg, produced much new material. Among the new species described were *E. barbeyanum* by Léveillé in 1907 and the highly distinctive *E. conjungens* by Skottsberg in 1906.

By 1923, partly under the impetus of a fine set of collections made by Erik Asplund in Bolivia, Gunnar Samuelsson had reviewed the entire genus in South America. He reworked nearly all of the material used by Haussknecht as well as more recent collections. As a result of his studies, he published many new taxa and recognized nearly all of those proposed by Haussknecht, bringing the total number of taxa to 34 species and 10 varieties.

Since that time very little has been published on South American *Epilobium*. Samuelsson, after studying collections in North American herbaria, reduced three taxa to synonymy (Samuelsson, 1930). Other, more recent works by Munz (1933, 1934, 1974), MacBride (1941), and a number of local floras have followed Samuelsson very closely.

Systematic Treatment

Epilobium L., Sp. Pl. 347. 1753, Gen. Pl., ed. 5, 164. 1754. LECTOTYPE: *Epilobium hirsutum* L., Britton & Brown, Ill. Fl. No. U.S. & Can., ed. 2, 2:590. 1913. (Complete synonymy not given.)

Chamaenerion Séguier, Pl. Veron. 3:168. 1754. LECTOTYPE: *Epilobium hirsutum* L., Holub, Folia Geobot. Phytotax. 7:84. 1972.

Zauschneria Presl, Rel. Haenk. 2:28, *pl. 52*. 1831. TYPE: *Z. californica* Presl.

Chamerion (Raf.) Raf., Herb. Raf. 51. 1833. Based on *Epilobium* subgen. *Chamerion* Raf., Amer. Monthly Mag. & Crit. Rev. 2:266. 1818. TYPE: *E. amenum* Raf.

Crossostigma Spach, Ann. Sc. Nat. Bot., ser. 2, 4:174. 1835. TYPE: *C. lindleyi* Spach, nom. illeg. = *E. minutum* Lindl. ex Lehm.

Pyrogennema Lunell, Amer. Midl. Naturalist 4:482. 1916. TYPE: *P. angustifolium* (L.) Lunell.

Cordylophorum (Nutt. ex Torr. & Gray) Rydb., Fl. Rocky Mts. 590, 1064. 1917. Based on *Epilobium* sect. *Cordylophorum* Nutt. ex Torr. & Gray, Fl. N. Amer. 1:488. 1840. TYPE: *C. suffruticosum* (Nutt.) Rydb.

Erect or creeping perennial or annual (3 species) herbs, sometimes woody at the base, overwintering and reproducing vegetatively by loose, scaly rhizomes, stolons, buds in the axils of leaves, soboles, leafy rosettes, or turions (fleshy, scale-leaved buds produced at or below the ground surface). Leaves simple, petiolate or sessile, opposite, at least at the lower nodes, alternate above, or all opposite, or all alternate in sect. *Chamaenerion*; pubescent or glabrous, the pubescence often distributed in descending lines on raised decurrent petiole margins. Flowers actinomorphic, or slightly zygomorphic in a few species, solitary in the axils of more or less reduced or unmodified leaves, clustered upwards, usually forming a few- to many-flowered, more or less discrete racemose, paniculate, or corymbose inflorescence, or scattered and few. Floral tube present or absent (sect. *Chamaenerion*). Sepals 4. Petals 4, white, cream, pink to rose pur-

ple, red, or yellow, emarginate or cleft. Stamens 8, the 4 antisepalous ones longer than the 4 antipetalous ones. Stigma capitate, clavate or deeply 4-lobed, protandrous or protogynous, or the anthers dehiscing at about the same time that the stigma becomes receptive. Capsule narrow, elongate or rarely narrowly clavate, 4-locular, loculicidal. Seeds many or rarely one or two in each locule, mostly obovoid, with a coma of long silky hairs at the chalazal (terminal) end that is rarely absent (1 species and some populations of a second). Gametic chromosome numbers: $n = 12$, 13, 15, 16, and 18, with polyploidy based on 15 and 18 in some taxa.

The generic description is based on the genus worldwide. As a result, some of the features given are not present in any of the South American species. The interested reader should refer to Raven (1976) and references therein for complete descriptions, discussion of generic and sectional delimitations, and synonymy.

Since it is now fairly well understood that the *Epilobium* species that occur in South America have had various and diverse origins, the arrangement of the taxa in a systematic treatment cannot be purely evolutionary. Instead, the species have been placed in what I believe to be more or less phyletic groups, beginning with those having the AA chromosomal arrangement, endemic and native, then the BB, endemic and native, and then those that have been introduced recently. *Epilobium paniculatum*, in sect. *Xerolobium*, by virtue of its primitive or distinctive features and lower chromosome number, might have been placed first. Because it is only sparingly introduced in South America, however, it has been placed at the end with the other introduced species. Neither descriptions nor keys have been prepared to distinguish the sections of *Epilobium*.

There are several points that must be kept in mind in order to understand fully the nature of the taxa enumerated here. Often there are great differences in the seasonal aspect of the plants. Those collected at the end of a growing season may be more branched, with few, often withered, lower leaves; and the flowers, fruits and seeds are often smaller than those produced by the same plant earlier in the season. Overwintering structures such as turions are frequently produced only near the end of a growing season, and may not be present. Or, as is often the case, specimens have been collected without regard to underground parts, even though they are taxonomically useful. Seeds from old or well dried specimens may be 10% smaller in both length and width than fresh, mature seeds (Raven & Raven, 1976). The dimensions given in the descriptions attempt to cover the full range of dry and fresh seeds.

Our understanding of the role of populations as evolutionary units has tended to broaden our view of what constitutes a species. In fact, considering the highly autogamous nature of most epilobiums, it is extremely questionable whether one can speak of more than a single plant as an evolutionary unit (Ehrlich & Raven, 1969; Levin & Kerster, 1974; Raven & Raven, 1976). Hence, the concept of a species or other taxon must be painted with a rather broad brush for it to be of any practical utility. This is fundamentally different from the approach taken in earlier times when many of the taxa in *Epilobium* were first given recognition. Plants that were at one time thought to be taxonomically distinct, I here may consider to be only a part of the "normal" variation within a polymorphic species or even a single population.

The descriptions and discussions have taken into account nearly all of the available herbarium material. With the exception of *E. conjungens* and *E. fragile*, all of the native species have been studied in the field, and one or more strains of each have been grown in greenhouses at the Missouri Botanical Garden.

A note of special significance for the nomenclature concerns the formae that Haussknecht used in his *Monographie* (Haussknecht, 1884). According to Raven (1962), the use of the feminine ending suggests that Haussknecht thought of his formae simply as organizational devices for the presentation of variation, and not as formal taxonomic units. Following this convention, the formae have been included in the synonymy only when they were taken up by later authors.

In the specimens examined, collections from Chile are placed in regions and provinces according to the most recent Atlas published by IGM (Instituto Geográfico Militar, 1980). This atlas follows the regionalization system implemented in 1973, which divided the country into 13 regions and 50 provinces. Specimens from other countries are placed according to the most recent maps available.

Key to the Species of *Epilobium* in South America

1a. Stems creeping, growing and rooting beyond the region of flower production, leaves all opposite; flowers few and scattered. Tierra del Fuego and adjacent islands. ---------- 12. *E. conjungens*

1b. Stems not creeping, erect, ascendent or decumbent, not growing and rooting beyond the flowers; leaves at least partly alternate; flowers few to many, in a more or less discrete inflorescence.

2a. Seeds broadly obovoid with a conspicuous constriction toward the micropylar end; floral bracts minute, fused to the pedicel; leaves often conduplicate, early deciduous, mostly alternate; annual. Western Neuquén and Chubut, Argentina. ---------- 15. *E. paniculatum*

2b. Seeds variously shaped, but without a conspicuous constriction; floral bracts leaf-like, reduced or not, but not fused to the pedicel, leaves flat, persistent, alternate or opposite; perennial, but usually flowering the first year.

3a. Plants glabrous (very rarely plants of *E. ciliatum* glabrous, but immediately distinguishable by their turions and longitudinally ridged seeds). Andes of Chile and Argentina.

4a. Plants low, caespitose; stems decumbent; leaves acute or obtuse, not glaucous. ---------- 6. *E. nivale*

4b. Plants robust, loosely rhizomatous, more or less clumped; stems erect; leaves acuminate, glaucous. ---------- 10. *E. glaucum*

3b. Plants variously pubescent, the hairs sometimes very sparse or restricted to the junction of the petiole bases.

5a. Upper stems hirsute or villous, and glandular, the hairs erect or slightly spreading.

6a. Leaves mostly alternate, opposite only at the lowest few nodes, coarsely serrate; inflorescence erect; petals white. Southern Brazil, Uruguay, eastern Argentina. ---------- 11. *E. hirtigerum*

6b. Leaves mostly opposite, alternate or subopposite only above or in the inflorescence, denticulate; inflorescence usually nodding; petals pink. Andes, Costa Rica to northern Chile and Argentina. ---------- 1. *E. denticulatum*

5b. Upper stems variously pubescent, but not hirsute or villous, the hairs not erect.

7a. Stems and ovaries densely erect glandular throughout, with some strigillose hairs; largest leaves with 3–5 teeth on each side; plants soboliferous or stoloniferous; seeds papillose. Central Andes of Chile and Argentina. ---------- 7. *E. barbeyanum*

7b. Stem and ovary pubescence various, if densely glandular then the leaves with more than 6 teeth on each side, or plants not soboliferous or stoloniferous; seeds variously sculptured.

8a. Leaves mostly alternate, opposite only at the lowest one or two nodes, or on very young shoots, coarsely and irregularly doubly serrate with uneven-sized teeth. Peru and Bolivia. ---------- 2. *E. pedicellare*

8b. Leaves mostly opposite or subopposite, alternate only above or in the inflorescence, denticulate or once serrate.

9a. Stems nearly glabrous, the pubescence a few scattered hairs, mostly at the fused petiole bases; plants low, <15 cm, densely caespitose. Peru, Bolivia and Chile. ---------- 3. *E. fragile*

9b. Stems variously pubescent, the pubescence more or less dense throughout; plants various.

10a. Plants densely caespitose, usually <15 cm tall, with a woody, contorted rootstock; flowers large, the petals 7–12 mm long; seeds 1.4–2.0 mm long. Central Andes of Chile and Argentina. -- 8. *E. densifolium*

10b. Plants loosely clumped or solitary, usually >15 cm tall; flowers large or small; seeds less than 1.4 mm long.

11a. Leaves narrowly ovate to ovate, thick, coarsely serrate with 4–8(–12) teeth on each side; plants not glandular. Andes of Chile and Argentina. ---------- 9. *E. australe*

11b. Leaves narrowly lanceolate to lanceolate, serrulate or denticulate, or if narrowly ovate, then the inflorescence glandular.

12a. Floral tube with a few, erect, glandular hairs, otherwise the plants not glandular (rarely also with a few on the upper portion of the ovary); largest leaves usually with 10 or more low denticulate teeth on each side; inflorescence erect. Central Chile. ---------- 13. *E. obscurum*

12b. Floral tube not glandular, or if glandular, then the glandular hairs also found on other plant parts, or minute and appressed; leaf margins various; inflorescence erect or nodding.

13a. Leaves serrulate, the largest usually with 10 or more teeth on each side, acuminate, the blade glabrous above and below; plants producing leafy rosettes or fleshy turions, the turions often persisting as a cluster of dead scales at the base of the stem.

14a. Seeds with longitudinal rows of flattened, fused papillae, at least along the sides; inflorescence glandular; lower stem smooth. Chile and Argentina. ---------- 5. *E. ciliatum*

14b. Seeds papillose, the papillae distinct; inflorescence not glandular; lower stems often with exfoliating epidermis. Central Chile. ---------- 14. *E. tetragonum*

13a. Leaves denticulate, acute or obtuse, usually with fewer than 10 low teeth on each side, if more than 10, then the inflorescence nodding, the blade more or less pubescent, the

hairs sometimes minute and appressed; plants without turions or basal rosettes, soboliferous or with leafy basal shoots.

15a. Stems with raised decurrent lines from the margins of the petioles; inflorescence and flowers nodding; younger leaves and upper stems usually with appressed to erect glandular or blunt-tipped hairs under higher magnification; petals pink to rose purple. Andes, Costa Rica to northern Chile and Argentina. ---------- 1. *E. denticulatum*

15b. Stems without raised decurrent lines from the margins of the petioles; inflorescence erect; leaves and stems not glandular; petals salmon pink. Central Chile. ---------- 4. *E. puberulum*

1. **Epilobium denticulatum** Ruiz & Pavón, Flora Peruviana et Chilensis 3:78, *tab. 314, f. 1–1a.* 1802. TYPE: Perú, Dpto. Junín, Tarma, 1779–1781, *H. Ruiz & J. Pavón* (MA, lectotype here designated, photograph MO; B (destroyed, photographs BH, MO), BM, F, G, OXF, isolectotypes). De Candolle, Prodromus 3:42. 1828. Hausskn., Monogr. *Epilobium* 264. 1884. Samuelsson, Svensk Bot. Tidskr. 17:250. 1923. MacBride, Field Mus. Nat. Hist., Bot. Ser. 8(4):530. 1941. Munz, Opera Bot. Ser. B, 3:6. 1974.

E. bonplandianum H.B.K., Nov. Gen. et Spec. Plant. 6:95. 1823. TYPE: Colombia, Dpto. Cauca, Andes de Popayán, Páramo de Puracé, 2,900 m, November–December 1801, *A. Humboldt & A. Bonpland s.n.* (P, lectotype here designated, photograph MO; P, isolectotype, photograph GH; F, HAL, P, probable isolectotypes). Humboldt & Bonpland, Synop. Plant. Aeq. 3:389. 1824. Hausskn., Monogr. *Epilobium* 267. 1884.

E. junceum Forst. f. ex Spreng., Syst. Veg. 2:233. 1825, nom. illegit. Based on *E. denticulatum* Ruiz & Pavón.

E. pedicellare auct. non Presl: Hook. & Arn., Bot. Misc. 3:309. 1833, pro parte.

E. caesium Hausskn., Oesterr. Bot. Z. 29:91. 1879. TYPE: Bolivia, Dpto. La Paz, Prov. Caupolicán, Pelechuco, 3,900–4,200 m, March 1865, *R. Pearce s.n.* (K, holotype, photograph MO). Hausskn., Monogr. *Epilobium* 268, *tab. 17, f. 75, 75a–c.* 1884.

E. andicolum Hausskn., Oesterr. Bot. Z. 29:118. 1879. TYPE: Bolivia, Dpto. La Paz, Prov. Larecaja, vicinity of Sorata, 1859, *M. G. Mandon 626* (K, lectotype here designated, photograph MO; BM, BR, GOET, K, P, isolectotypes). *Mandon 626* is apparently a distribution number. From an examination of the many sheets available, it is probable that several gatherings were included. The lectotype and isolectotypes are limited to those specimens annotated as *E. andicolum* by Haussknecht. Hausskn., Monogr. *Epilobium* 266, *tab. 17, f. 76, 76a–c.* 1884. Samuelsson, Svensk Bot. Tidskr. 17:255. 1923; Svensk Bot. Tidskr. 24:2. 1930.

E. meridense Hausskn., Oesterr. Bot. Z. 29:148. 1879. TYPE: Venezuela, Est. Mérida, Sierra Nevada, 3,300 m, August 1842, *J. Linden 418* (W, lectotype here designated, photograph MO; BM 2 sheets, BR (probable), F, G (photographs BH, MO), K, OXF, P 2 sheets, TCD, W, isolectotypes). Hausskn., Monogr. *Epilobium* 266. 1884. H. Lév., Iconogr. *Epilobium tab. 193, 194.* 1911. Samuelsson, Svensk Bot. Tidskr. 17:257. 1923; Svensk Bot. Tidskr. 24:9. 1930. Munz, Aliso 4:488. 1960; N. Amer. Fl. II 5:218. 1965; Opera Bot., Ser. B, 3:7. 1974. Vareschi, Flora de Los Páramos 247, *f. 77.* 1970.

E. helodes H. Lév., Bull. Herb. Boissier, sér. 2, 7:589. 1907. TYPE: Colombia, Dpto. Tolima, Páramo de Ruiz, high montane forest, 3,000 m, 11 September 1883, *F. C. Lehmann 3158* (G, holotype, photograph MO; BM, US, isotypes). *E. meridense* var. *helodes* (H. Lév.) Samuelsson, Svensk

Bot. Tidskr. 17:258. 1923. Samuelsson, Svensk Bot. Tidskr. 24:10. 1930. Munz, Opera Bot., Ser. B, 3:7. 1974.

E. denticulatum var. *aberans* Samuelsson, Svensk Bot. Tidskr. 17:253. 1923. TYPE: Bolivia, Dpto. La Paz, Prov. Aberoa, Challapata, 3,750 m, 31 March 1921, *E. Asplund 3250* (UPS, holotype, photograph MO; S, isotype).

E. denticulatum var. *confertum* Samuelsson, Svensk Bot. Tidskr. 17:252. 1923. TYPE: Ecuador, Prov. Pichincha, Quito, 1847, *W. Jameson 192* (W, lectotype, photograph MO; BM, G, S, TCD, US, isolectotypes; P. Munz, Opera Bot., Ser. B, 3:6. 1974).

E. denticulatum var. *macropetalum* Samuelsson, Svensk Bot. Tidskr. 17:253. 1923. TYPE: Perú, Dpto. Cuzco, Pacechac, near Río Urubamba, 4,500 m, 3 March 1903, *A. W. Hill 155* (K, lectotype; P. Munz, Opera Bot., Ser. B, 3:6. 1974).

E. asplundii Samuelsson, Svensk Bot. Tidskr. 17:256, *tab. 3, f. 2.* 1923. TYPE: Bolivia, Dpto. La Paz, Prov. Omasuyos, Challa, Isla del Sol, 3,850 m, 18 April 1921, *E. Asplund 3708* (UPS, holotype, photographs MO, S).

E. meridense var. *condensatum* Samuelsson, Svensk Bot. Tidskr. 17:258. 1923. TYPE: Ecuador, Prov. Chimborazo, El Altar, 3,900–4,000 m, July 1903, *H. Meyer 174* (JE, lectotype here designated, photograph MO; JE, isolectotype). All of the material cited by Samuelsson was located at Berlin (B) and is now destroyed. The lectotype has been selected from the duplicates of that material at other institutions.

E. aequinoctiale Samuelsson, Svensk Bot. Tidskr. 17:259, *tab. 2, f. 1.* 1923. TYPE: Colombia, Dpto. Nariño, Túquerres, 1844–1847, *H. Karsten* (W, lectotype here designated, photographs BH, MO, S; JE, isolectotype). H. Lév., Iconogr. *Epilobium tab. 198* (as *E. repens*). 1911. Munz, Opera Bot., Ser. B, 3:4. 1974.

E. assurgens Samuelsson, Svensk Bot. Tidskr. 17:261, *tab. 5, f. 2.* 1923. TYPE: Ecuador, Prov. Tunguragua, Volcán Tunguragua, "Locis paludosis," May 1858, *R. Spruce 5389* (W, lectotype here designated, photographs BH, MO, S; BM, K 2 sheets, NY, OXF, TCD, W, isolectotypes). Samuelsson, Svensk Bot. Tidskr. 24:3. 1930.

E. bolivianum Samuelsson, Svensk Bot. Tidskr. 17:263, *tab. 2, f. 3.* 1923. TYPE: Bolivia, Dpto. La Paz, Prov. Murillo, stream at La Cumbre, 4,600 m, 26 May 1921, *E. Asplund 4014* (UPS, holotype, photographs MO, S; B (destroyed, photographs BH, MO, US), S, W, Z, isotypes). MacBride, Field Mus. Nat. Hist., Bot. Ser. 8(4):530. 1941.

E. deminutum Samuelsson, Svensk Bot. Tidskr. 17:264, *tab. 4, f. 5.* 1923. TYPE: Bolivia, Dpto. La Paz, Prov. Murillo, Nevado Huayna-Potosí, Glaciar Franz Josefs, *Germann 24* (W, holotype, photographs BH, MO, US, fragment UPS). Samuelsson, Svensk Bot. Tidskr. 24:5. 1930.

E. hirtum Samuelsson, Svensk Bot. Tidskr. 17:266, *tab. 2, f. 2.* 1923. TYPE: Bolivia, Dpto. La Paz, Prov. Murillo, San Jorge, now within the city of La Paz, 3,500 m, 1 November 1920, *E. Asplund 666* (UPS, lectotype here designated, photographs MO, S; S, isolectotype). Samuelsson, Svensk Bot. Tidskr. 24:4. 1930. MacBride, Field Mus. Nat. Hist. Bot. Ser. 8(4):532. 1941.

Variable, clumped perennial herbs (10–)20–70(–160) cm tall, reproducing vegetatively by elongate, leafy shoots or soboles produced at or near the base. Stems erect or ascendent, several to many, mostly simple, occasionally branched above, and often from the base, strigillose to spreading hirsute, with hairs 0.1–0.4 mm long, often with an admixture of appressed to erect glandular hairs, 0.05–0.2 mm long, at least in the inflorescence. Leaves mostly opposite, alternate above and in the inflorescence, thin, green, occasionally reddish purple, especially along the veins and margins, lanceolate, occasionally ovate, rarely broadly so, 1–5.6 cm long, 0.2–1.7 cm wide, acute to acuminate, rarely obtuse at the apex, denticulate with 3–8(–13) low teeth on each side, acute to cuneate, occasionally obtuse or rounded at the base, strigillose to spreading hirsute on the abaxial and adaxial veins and midrib, or thinly scattered on the blade, with scattered appressed to spreading blunt-tipped or glandular hairs, 0.05–0.2 mm long, occasionally densely so, the lateral veins prominent, 2–4(–5) on each side of the midrib, on petioles 0.5–2(–4) mm long, rarely sessile. Inflorescence simple, nodding, the leaves subtending the flowers usually slightly reduced in size. Flowers nodding at anthesis. Ovaries often reddish or purplish, strigillose to spreading hirsute, often densely so, usually with an admixture of appressed to spreading glandular hairs, 0.9–2.2

cm long, on pedicels 2–5(–8) mm long. Floral tube often reddish purple, 0.8–2 mm deep, 1.5–3(–4) mm across, externally strigillose to spreading hirsute, usually with appressed to spreading glandular hairs, internally with a ring of erect villous hairs 0.1–0.2 mm long, sometimes reduced to only a few, or occasionally glabrous. Sepals often reddish purple, lanceolate, 2.2–5.7(–7) mm long, 1.1–2.1 mm wide, strigillose to spreading hirsute, usually with appressed to spreading glandular hairs. Petals pale pink to rose purple, occasionally white or nearly so, obovate, rarely broadly so, (2.5–)3.5–7.6(–9.5) mm long, (2–)2.7–4(–6.1) mm wide, the notch 1.1–2 mm deep. Anthers cream to white, or slightly pinkish, 0.6–1.6 mm long, 0.4–0.9 mm wide; filaments bluish purple to pale lavender, those of the longer stamens (1.4–)1.8–3.2(–4.4) mm long, those of the shorter (0.7–)1.5–2.8 (–3.2) mm long; the longer stamens, and often the shorter, shedding directly on the stigma at anthesis, or held away and bending toward the stigma after anthesis in some populations. Style white to slightly bluish, (2.2–)3.5–6.3(–9) mm long; stigma white, capitate to clavate, 1.1–2 mm long, 0.8–1.2 mm thick, occasionally exserted beyond the anthers. Capsules erect, strigillose to spreading hirsute, usually with appressed to erect glandular hairs, often glabrate or glabrous, 3.5–7 (–8.5) cm long, 1.3–1.7 mm thick, on pedicels 0.3–2.5(–3.4) cm long. Seeds brown, papillose, obovoid, 0.8–1.1 mm long, 0.35–0.45 mm thick, the chalazal end with a short appendage, 0.04–0.1 mm long, 0.08–0.14 mm wide; coma white to slightly yellowish, 4–7 mm long. Gametic chromosome number, $n = 18$.

Distribution (Fig. 1): A widespread, weedy species that grows along stream banks, seeps, bogs, moist embankments, roadsides, or other open disturbed sites, mostly in the páramos and puna of the high Andes but also extends into forested zones. In South America throughout the northern and central Andes from the páramos of Venezuela and Colombia, including the Sierra de Santa Marta and the Sierra de Perijá, southward through Ecuador; widely distributed in the altiplano of Perú, Bolivia, northeastern Chile, and northwestern Argentina, continuing southward along the eastern side of the Andes to central Mendoza Prov., Argentina; disjunct in the Sierra de San Luis and the Sierra Grande de Córdoba. In North America restricted to the Sierra de Talamanca, Costa Rica. Found growing between 2,500 and 4,800 m throughout most of its range, descending to lower elevations along roads in forested zones, or along rivers in drier areas; at its southern limit typically between 1,800 and 3,000 m, and in the Sierra Grande de Córdoba between 1,200 and 2,500 m. Flowering throughout the year from Venezuela to Peru; however, from Bolivia southward there is a marked suppression of flowering during the coldest, driest months (July and August in Bolivia) and therefore in the southernmost parts of its range, flowering occurs between December and March.

Representative specimens examined: ARGENTINA, CATAMARCA: Dpto. Ambato, Sierra de Ambato, Casa de Cubas, 3,000 m, *Hunziker & DeFulvio 19828* (CORD, MO); Dpto. Pomán, Las Casitas, Sierra de Ambato, 2,500 m, *Hunziker & Ariza 20424* (CORD, MO); Dpto. Capayán, Los Angeles, *Russo 792* (LIL); Belén, Quebrada de Los Potrerillos, 2,600 m, *Sleumer & Vervoorst 2461* (US). CÓRDOBA: Dpto. San Javier, Quebrada del Tigre, 1,800 m, *Bridarolli 1440* (LP); Pampa de Achala, Los Gigantes, *Castellanos in 1924* (BA); Sierra Achala, Cuesta de La Sala Grande, *Hieronymus 856* (CORD, F, US); Sierra Grande, Cuesta de Copina, *Hunziker 8738* (CORD, MO, RSA); Sierra Grande, E slope Cerro Champaqui, *Hunziker 9618* (CORD, MO, RSA); La Cumbrecita, 1,450 m, 31°55′S, 64°15′W, *Solomon 4192* (MO). JUJUY: *Dpto. Yavi*, Quebrada de Toquero, 3,600 m, 22°18′S, 65°36′W, *Cabrera et al. 15380* (BAB, LP, M); Dpto. Tumbaya, Volcán Chilcayo, 23°43′S, 65°40′W, *Fabris et al. 6290*

FIGURE 1. Distribution of *Epilobium denticulatum*.

(LP). Dpto. Tilcara, Quebrada del Abra de la Cruz, *Fabris et al. 6353* (BAA, LP); Dpto. Valle Grande, Caspalá, 3,000 m, 23°19′S, 65°08′W, *Fabris & Crisci 6925* (LP); Dpto. Tumbaya, Angosto del Chañi, 3,900 m, *Kiesling et al. 298* (LP); Dpto. Humahuaca, Río Despensas, 4,000 m, *Ruthsatz IV60* (BAA, MO). LA RIOJA: Dpto. Famatina, Los Corrales, *Cabrera et al. 27254* (BAB, SI); Dpto. Famatina, Sierra Famatina above La EnCrucijada, 3,200 m, 28°58′S, 67°42′W, *Hawkes et al. 3404* (C); Sierra de

Famatina, Cueva de Medina, 3,100 m, *Krapovickas 6163* (BAB, CORD). MENDOZA: Quebrada de Alvarado, 3 km S of Chilicito, 1,550 m, *Hjerting 6322* (C); Dpto. Tunuyán, 10 km W of Campo de Los Andes, 1,500 m, *Melis & Barkley in 1950* (LIL); Dpto. Tupungato, Río La Carrera, 2,350 m, *Sleumer 427* (B). SALTA: Dpto. Calayate, Sierra de Los Quilmes, 2,400 m, *Castellanos in 1943* (BA, RSA); Nevado Castillo, 25°11′S, 65°21′W, *Lorentz & Hieronymus 88* (CORD, F, GOET, JE, S, US); Dpto. Guachipas, Pampa Grande, 1,600 m, 25°40′S, 65°30′W, *Hunziker 1820* (POM); Dpto. Santa Victoria, Santa Victoria, 2,385 m, *Meyer 4962* (F, UC). SAN JUAN: Dpto. Iglesia, Cordillera Agua Negra, Piedras Negras, 30°16′S, 69°47′W, *Castellanos in 1950* (US); Dpto. Iglesia, Vega de Santa Rosa, 3,300 m, 29°00′S, 69°15′W, *Hunziker & Caso 4791* (BAB, CORD); Cienaga de Las Cabeceras, 2,700 m, 31°47′S, 69°07′W, *Kurtz 9808* (BAF, CORD). SAN LUIS: Pancanta, 32°59′S, 66°11′W, *Castellanos in 1925* (BA); Sierra de San Luis, Arroyo de Las Aguilas, *Vignati 101* (LP). TUCUMÁN: Dpto. Tafi, Lara, 3,200 m, *Rodríguez 310* (BA, BAF, GH, MO, RSA, S, SI); Dpto. Chicligasta, Estancia Las Pavas, Río Cascada, 2,700 m, *Venturi 3033* (BA, BAB, DS, GH, MO, SI); Dpto. Tafi, Cerro San José, 2,700 m, *Venturi 3573* (BA, BAB, DS, GH, RSA, SI, US); Dpto. Chicligasta, Estancia Santa Rosa, 3,300 m, *Venturi 4787* (BA, BAB, LP, MO, SI).

BOLIVIA, COCHABAMBA: Cona-Cona, 4,000 m, 18°00′S, 66°45′W, *Brooke 5181* (BM); Vila-vila, 18°00′S, 65°30′W, *Brooke 5859* (BM, F, NY); Between Chimore and Cochabamba, Km 80, 3,000 m, 16°42′S, 64°49′W, *Cárdenas 760* (LIL, US). Prov. Ayopaya, Sailapata, 2,700 m, 16°30′S, 66°35′W, *Cárdenas 3057* (BR, F, P, S, US). Prov. Cercado, Sierra Tunari near Lago Huara-Huara, 17°12′S, 66°10′W, *Hawkes & Hjerting 6606* (C, MO). Prov. Quillacollo, 28 km from Quillacollo on road to Morochata, 3,850 m, 17°19′S, 66°22′W, *Hawkes & Hjerting 6692* (C). 35 km W of Comarápa on road to Cochabamba, 2,700 m, *King & Bishop 7654* (MO, US). Prov. Carrasco, 2 km above Siberia, 3,200 m, *Steinbach 210* (F, GH, MO, NY, US, WIS). Prov. Ayopaya, Puente San Miguel, 25 km NNW of Cochabamba, 3,800 m, 17°10′S, 66°25′W, *Ugent 4781* (DS, GH, MSC, UC, US, WIS). LA PAZ: Prov. Murillo, entre Pongo and La Rinconada, 4,000 m, *Asplund 1818* (S, UPS). Prov. Ingavi, Guaqui, *Asplund 2305* (S, UPS, Z). Prov. Pacajes, General Campero, 3900 m, 17°27′S, 68°58′W, *Asplund 2791* (UPS). Prov. Omasuyos, Isla del Sol, Challa, 3,850 m, *Asplund 3709* (S, UPS). Vicinity of La Paz, 3,000 m, *Bang 75* (E, G, GH, MO, NY, PH, US). Prov. Murillo, Palca, 5 km hacia la mina San Francisco, 4,800 m, *Beck 2223* (MO). Prov. Ingavi, Huacullani, 3,840 m, *Beck 2470* (MO). Mina La Fabulosa, 4,600 m, 16°00′S, 68°00′W, *Brooke 6329* (BM, NY). La Paz, *Buchtien in 1919* (ARIZ, BM, BP, C, LD, E, F, G, GH, M, MO, NY, S, US, Z); *in 1930* (BM, C, E, G, K, M, MO, S, Z). 30 km SW of Yoloso on road to Unduavi, 2,900 m, *Davidson 4968* (LAM). Prov. Larecaja, vicinity of Sorata, *Mandon 626* (F, G, GH, GOET, JE, MICH, MO, MPU, NY, PR, S, US, W); *Williams 1549* (BM, NY). Yungas, 1,800 m, *Rusby in 1885* (F, GH, MICH, NY, PH, US, WIS). Valle de Hichucota, Laguna Kkota, 4,500 m, 16°07′S, 68°20′W, *Solomon 4938* (MO). Valle de Hichucota, 4,150 m, *Solomon 5007* (MO); 11.3 km NE of La Paz on road to Unduavi, 4,400 m, *Solomon 5013* (MO). La Cumbre on road to Unduavi, 4,600 m, 16°20′S, 68°03′W, *Solomon 5028* (MO). 6 km W of Palca on Placa-La Paz road, 3,800 m, 16°32′S, 67°58′W, *Solomon 5139* (MO). Upper Valle de Zongo, 3,000 m, 16°10′S, 68°09′W, *Solomon 5243* (MO). Prov. Murillo, Valle de Achocalla, 3,800 m, 16°35′S, 68°11′W, *Solomon 5298* (MO). POTOSÍ: Between Quechisla and Chorolque, 3,600 m, 20°56′S, 66°01′W, *Cárdenas 304* (US). Lagunillas, 3,800 m, *Cárdenas 410* (US). SANTA CRUZ: Near Valle Grande, 2,600 m, *Cárdenas 5138* (US). TARIJA: Iscayache, 3,600 m, *Fiebrig 3015* (BM, E, G, CH, GOET, L, M, P, PR, PRC, S, US, W). Rincón de la Victoria, 17 km W of Tarija, *Krapovickas et al. 18880* (CTES).

CHILE, I REGIÓN (TARAPACÁ): *Arica,* Camino de Arica al Portezuelo de Chapiquiña, Km 99, 3,500 m, 18°19′S, 69°31′W, *Marticorena et al. 59* (CONC, MO), *98* (CONC); Al interior de Chitita, 2,500 m, 18°49′S, 69°41′W, *Schlegel 5100* (MO). *Iquique,* Al interior de Coscaya, 3,360 m, 19°51′S, 69°09′W, *Ricardi et al. 418* (CONC, MO); Quebrada de Quipisca, Noasa, 3,500 m, 19°59′S, 67°08′W, *Werdermann 1060* (BM, CAS, E, F, G, GH, LIL, MO, NY, S, SI, U, UC, US, Z); Chusmiza, 19°41′S, 69°11′W, *Zöllner 2947* (MO). *Parinacota,* Socoroma, 3,300 m, 18°15′S, 69°37′W, *Richardi et al. 190* (CONC, MO). II REGIÓN (ANTOFAGASTA): *Antofagasta,* Sierra Almeida, Aguada Chocas, 3,700 m, 24°15′S, 68°35′W, *Biese 2337* (LIL), *2388* (LIL). *El Loa,* Caspana, 22°20′S, 68°14′W, *Mahu in 1969* (LD); Toconoa, 23°11′S, 68°01′W, *Pfister in 1950* (CONC).

COLOMBIA, ANTIOQUIA: Páramo Frontino, Cerro de Campanas, 3,650 m, 6°28′N, 76°04′W, *Boeke & McElroy 302* (MO, NY). BOYACÁ: Sierra Nevada del Cocuy, Laguna de San Pablo, 3,850 m, *Grubb et al. 107* (COL, K, MSC, US); Quebrada Surbar, between Duitama and Charalá, 3,273 m, *Langenheim 3537* (COL, UC, US). CALDAS: Nevado del Ruiz, entre Termales y Líbano, *Barclay & Juajibioy 6380* (COL, MO, RSA); Pinares, above Salento, 2,800 m, *Pennell 9347* (GH, NY, PH, US); Páramo del Quindo, 3,700 m, *Pennell & Hazen 9989* (GH, NY, PH, S, US, WU). CAUCA: Between Guachicono and Río Putis, 2,500 m, *Core 933* (RSA, US); Páramo de Las Papas, El Boquerón, *Idrobo et al. 3014* (COL); San Antonio, 2,300 m, *Pennell 7653* (GH, NY, PH, US); Entre Popayán y Puracé, Río Anambio, 2,500 m, *Pérez & Cuatrecasas 5869* (COL, US). CUNDINAMARCA: 15 km N of Usaquén, 2,600 m, *Haught 6205* (COL, US); 20 km NE of Bogotá, 2,470 m, *Luteyn et al. 4809* (COL, F, MO, NY, US); Zipaquira, 2,650 m, *Pennell 2542* (F, GH, MO, NY, US). HUILA: Moscopán, Santa Leticia,

2,230 m, *Garcia-Barriga & Hawkes 12893* (COL, LIL, RSA, US); Balsillas, on Río Balsillas, 2,000 m, *Rusby & Pennell 728* (F, GH, MO, NY, US). MAGDALENA: Sierra Nevada de Santa Marta, Hoya del Río Donachuí, 3,600 m, *Cuatrecasas & Castañeda 24538* (COL, US); Sierra de Santa Marta, Paso de Mamancanaca-Cambiremena, 3,800 m, *Weston 10391* (MO). META: Páramo de Sumapaz, 4,100 m, *Cleef 7987* (COL, MO); Río Arroz above Quebrada Pedregal, 3,445 m, *Fosberg 20911* (RSA, US). NARIÑO: 31 km E of Pasto on road to Sibundoy, *Berry 3253* (MO); Volcán Galera, Hacienda Obonuco, *Espinosa 2777* (CAS, DS, RSA); Volcán de Cumbal, near Laguna Bolsa, 2,930 m, *Ewan 16138* (BM, POM, RSA, US); Páramo del Tábano-Putúm, *Garcia-Barriga 4552* (COL); Camino de Túquerres a La Chorrera, 3,000 m, *Mora 755* (AAU, COL). NORTE DE SANTANDER: Valley of Río Chitaga, SW of Pamplona, 2,600 m, *Fassett 25958* (RSA, US); Laso, N of Toledo, 2,400 m, *Killip & Smith 20391* (F, GH, NY, S, US). PUTUMAYO: Valley of Sibundoy, Portachuelo, 2,400 m, *Schultes & Villarreal 7736* (COL, ECON, F, GH, US); Between La María and Páramo de San Antonio, 2,900 m, *Schultes & Villarreal 7832* (COL, GH, LIL, US); Páramo de Quilisayaco, 3,300 m, *Uribe 5380* (COL, NY). SANTANDER: Berlín, 3,100 m, *Enrique et al. 577* (COL, MO); Páramo de Las Vegas, 3,300 m, *Killip & Smith 15715* (BM, F, GH, NY, P, S, US); Páramo de Mogotocoro, 3,700 m, *Killip & Smith 17647* (GH, NY, US); Alto del Almorzadero, 3,840 m, 6°59′N, 72°39′W, *St. John 20802* (GH, MICH, NY, RSA, S, UC, US). TOLIMA: 41 km E de Manizales, 3,250 m, *Forero et al. 3662* (COL, MO); Quindío Highway, W of Cajamarca, 3,200 m, *Killip & Varela 34554* (BM, COL, GH, S, US); Páramo de Ruiz, 3,400 m, *Pennell 3070* (GH, NY, US). VALLE: Hoya del Río Tuluá, entre Las Vegas y La Ribera, 3,300 m, *Cuatrecasas 20430* (F, RSA); Río Cali, Pichinde, 1,700 m, *Duque-Jaramillo 4183* (COL).

COSTA RICA, CARTAGO-SAN JOSÉ: Cerro de la Muerte, ca. 5 km above Villa Mills, 3,400 m, *Allen & Dodge 5680* (F, G, US), *Holm & Iltis 469* (A, F, G, UPS), *Whitmore 39* (F, MO, NY); La Asunción, 32 km N of San Isidro del General, 3,335 m, 9°34′N, 83°45′W, *Burger & Stolze 5989* (F), *Wilbur 21237* (DUKE); 8 km S of Taja, *Tessene 1474* (WIS); Cerro Buena Vista, *Weaver 1413* (DUKE).

ECUADOR, AZUAY: Nudo de Portete, 2,700 m, *Camp E-2169* (NY); Lago Zurru Cuchu, 3,700 m, *Prescott 829* (NY); Nabón, 3°20′S, 79°04′W, *Rose 23016* (US). BOLÍVAR: Western slopes of Volcán Chimborazo, 3,600 m, *Harling et al. 9632* (GB, MO, RSA); Simiatug, Hacienda Talahua, 3,200 m, *Penland & Summers 628* (F, GH). CAÑAR: El Tambo, 69 km S of Sibambe, 3,000 m, *Camp E-3982* (G, GH, MO, NY, P, RSA, UC, US); Cerro Buerán, 5 km S of Cañar, 3,600 m, *Fosberg & Giler 22639* (NY, US). CARCHI: Valle de Maldonado, 53 km W of Tulcán, 3,100 m, 0°50′N, 78°03′W, *Holm-Nielsen et al. 5570* (AAU, F, MO, NY, S, U); Páramo El Angel, 3,500 m, 0°41′N, 77°54′W, *Holm-Nielsen et al. 5289* (AAU, COL, F, MO, NY, S, U). CHIMBORAZO: Guamote, 3,000 m, *Asplund 6878* (CAS, G, S, UPS, US); Between Chunchi and Sibambe, 2,200 m, *Fagerlind & Wibom 783* (S); Páramo de Tililac, 3,600 m, *Harling et al. 6573* (GB, RSA); 14 km S of Mocha, 3,800 m, 1°29′S, 78°43′W, *Iltis E-481* (MO, WIS). COTOPAXI: 29 km E of Salcedo on Salcedo-Napo road, 3,860 m, *Boeke 778* (MO, NY); Pilalo-Latacunga road, 3,400 m, *Holm-Nielsen & Jeppesen 1477* (AAU, C, DS, NY, S); Volcán Cotopaxi, Hacienda Yacu-Tambo, 3,659 m, *Ugent & Albornoz 5672* (DS, MSC, UC, US, WIS). IMBABURA: Lago Cuicocha, Islote Chica, 3,080 m, *Asplund 7161* (S); Río San Marcos, E of Volcán de Cayambe, 3,350 m, *Drew E-183* (C, COL, RSA, US); Mojanda, 10 km SSW of Otavalo, 2,900 m, 0°10′N, 78°18′W, *Sparre 13463* (S). LOJA: Loja, Angelica, 2,300 m, *Espinosa 363* (RSA); Lado sur de Saraguro, 2,300 m, *Espinosa 1386* (POM); Near Yangana, 2,000 m, *Hart 1032* (MO). MORONA-SANTIAGO: Entre Gualaceo y General Plaza, Km 29, 3,000 m, *Sparre 18777* (S). NAPO: Km 216 on Quito-Papallacta road, 3,700 m, *Berry 2522* (MO); Cerro Antisana, 4,000 m, 0°30′S, 78°00′W, *Grubb et al. 575* (DS, MSC, NY); 10 km E of Papallacta, 2,800 m, 0°21′S, 78°01′W, *Holm-Nielsen et al. 6839* (AAU, MO, NY, S). PICHINCHA: Tumbaco, 2,450 m, *Asplund 6554* (S); Pichincha, 3,650 m, *Asplund 6581* (S); Valle de La Magdalena, Chillogallo, 2,800 m, *Firmin 99* (F, S, US); Quito, *Humboldt & Bonpland in 1801* (F, P, RJ); Volcán Pichincha, *Sodiro in 1871* (BP, JE); Lagunita Linda, 3 km W of Paso de Guamaní, 3,900 m, *Sparre 15063* (S); W of Mt. Iliniza, 3,320 m, *Weydahl 153* (S). TUNGURAHUA: Patate, Hacienda Leito, 2,900 m, *Asplund 7961* (S); 10 km S of Mocha, 3,500 m, *Harling 6938* (GB); Vicinity of Ambato, Ficoa, *Pachano 145* (GH, NY, US); Río Colorado, Volcán Chimborazo, 4,200 m, *Sparre 18364* (S). ZAMORA CHINCHIPE: 20 km E of Loja on road to Zamora, 2,350 m, *Mathias & Taylor 5195* (RSA).

PERÚ, AMAZONAS: Chachapoyas, 6°13′S, 77°51′W, *Matthews in 1834* (BM, BR, E, K, OXF); Prov. Bongará, hills WNW of Pomacocha, 2,700 m, 5°50′S, 77°55′W, *Wurdack 924* (F, NY, RSA, UC, US). ANCASH: Cordillera Negra, Callán, 4,200 m, *Bernardi 16676* (G); Prov. Bolognesi, Parientana, E of Chiquián, 3,420 m, 10°09′S, 77°11′W, *Ferreyra 5659* (MO, US, USM); Prov. Carazi, Laguna Parón, 4,100 m, 9°10′S, 77°35′W, *Mostacero et al. 547* (MO, NY). APURIMAC: Prov. Abancay, 16 km E of Abancay on Cuzco road, 3,000 m, *Iltis & Ugent 641* (DS, WIS); Prov. Andahuaylas, Mollebamba, 3,650 m, *Vargas 8721* (LIL). AREQUIPA: 20 km W of Arequipa, *Averett 1004* (MO); S slopes of Nevado Chachani, *Hinkley 65* (CAS, GH, NY, US); Prov. Cailloma, 15 km NE of Chivay, *Mueller et al. 2221* (LZ); Arequipa, Río Chili, 2,500 m, *Munz 15511* (F, GH, NY, POM); Pichu-Pichu, 3,000 m, 16°29′S, 71°15′W, *Sandeman 3758* (K, OXF); Prov. Condesuyos, Chuquibamba, 3,350 m, *Stafford 1165* (BM, F, K). AYACUCHO: Prov. Huanta, mountains NE of Huanta, 3,200 m, *Weberbauer 7505*

(F, GH, NY, US, WIS). CAJAMARCA: Prov. Contumazá, Lledén, 2,600 m, *Sagástegui et al. 9408* (MO); Prov. Cajamarca, Granja Porcón (SIPA), 28 km NW of Cajamarca, 3,260 m, *Ugent 5454* (DS, UC, WIS). CUZCO: Prov. Quispicanchis, Marcapata, 3,000 m, 13°30′S, 70°55′W, *Berry & Aronson 3020* (MO); Sicuani, 3,551 m, *Hicken in 1903* (BAF, SI); Pampa de Anta, 7 km W of Anta, Ancahuasi, 3,150 m, *Iltis & Ugent 783* (DS, MSC, UC, WIS); Cordillera Vilcabamba, Río Raccachaca, 4,500 m, *McSweeney in 1976* (MO); Ollantaitambo, *Munz 15544* (NY, POM, US, WTU), *Pennell 13670* (F, GH, NY, PH, S, US); La Raya, 4,400 m, *Pennell 13514* (F, PH); Entre Paucartambo y Tres Cruces, Cerro de Cusilluyoc, 3,400 m, *Pennell 14157* (F, GH, PH); Ausangate, 4,700 m, *Rauh-Hirsch P1151* (RSA); 4 km NE of Cuzco on road to Pisac, 3,500 m, *Ugent 4098* (DS, GH, MICH, MSC, UC, US, WIS); Prov. Paucartambo, 5 km NE of Paucartambo, 2,900 m, *Ugent & Vargas 4407* (DS, US, WIS); Prov. Espinar, Huaillapacheta, 14°45′S, 71°25′W, *Vargas 6507* (CAS, LIL); Prov. Cañas San Andres de Checca, 3,860 m, 14°25′S, 71°20′W, *Vargas 11014* (F, NA, UC); Prov. Urubamba, Cañón Chicón, 2,900 m, *Vargas 11054* (F, GH, NA, UC). HUANCAVELICA: San José de Acobambilla, 3,700 m, 12°40′S, 75°22′W, *Lloyd et al. 536* (K); Prov. Tayacaja, Pampas, 3,250 m, *Stork & Horton 10236* (F, G, GH, NA, UC); Prov. Huancavelica, Machajhuay between Conaica and Tinyajlla, 3,800 m, *Tovar 801* (MO). HUANUCO: 9 km from Chirlín, 3,660 m, *Gentry et al. 19214* (MO); Tambo de Vaca, 3,900 m, 9°42′S, 75°47′W, *MacBride 4373* (F, GH, S, US); Pillao, 2,700 m, 9°40′S, 75°58′W, *Woytkowski 34119* (F, GH, MO, UC). JUNÍN: Oroya, 3,700 m, *Kalenborn 19* (DS, GH, MO, US). Prov. Yauli, Lago Huacracocha, 3,750 m, 11°40′S, 76°10′W, *López & Riccio 10820* (RSA); Tarma, Hacienda Maco, 3,600 m, *Ochoa 238* (CORD, NY). LA LIBERTAD: 70 km E of Trujillo, between Pampa and Yamobamba, 3,050 m, *Conrad 2715* (MO); Entre Motil y Quiruvilca, Km 104–105, 3,300 m, *Ferreyra 3026* (MO, USM); Prov. Patazi, entre Huancaspata y Tayabamba, 3,800 m, *López & Sagástegui 8262* (MO). LIMA: Prov. Yauyos, Huancracha, 3,300 m, *Cerrate 1180* (MO, USM); Río Blanco, 3,000 m, *Killip & Smith 21579* (F, NY, S, US); *MacBride & Featherstone 677* (F, GH, K, S, US); Prov. Huarochiri, Casapalca, 4,700 m, *MacBride & Featherstone 857* (F, GH, S, US). MOQUEGUA: Saylapa, near Carumas, 3,300 m, 16°49′S, 70°43′W, *Weberbauer 7337* (F, S). PASCO: La Quinua, 3,600 m, 10°33′S, 76°10′W, *MacBride & Featherstone 2023* (F, GH, S, US); Paucartambo, 2,800 m, *Woytkowski 6711* (GH); Cerro de Pasco, 4,130 m, *Ellenberg 411* (MO). PUNO: Amantani, 3,900 m, 15°32′S, 70°01′W, *Aguilar 234* (MO, USM); Prov. Azángaro, Cala-Cala, 4,100 m, 15°14′S, 70°33′W, *Bernardi 16745* (G); between Ollachea and Macusani, *Dillon et al. 1266* (MO); Prov. Sandia, 2–6 km S of Limbani, 3,550 m, *Metcalf 30452* (UC, US); Santa Rosa, 80 km SSW of Ilave, 4,300 m, *Pearson 33* (PH); Araranca, 4,100 m, *Pennell 13432* (F, GH, NY, PH, S, US); Prov. Huancané, Occa Pampa, 3,965 m, 15°10′S, 69°35′W, *Shepard 78* (GH, NY, US); 16 km NE of Macusani, 4,600 m, *Webster 2* (K). SAN MARTÍN: Prov. Huallaga, valley of Río Apisoncho, 30 km above Jucusbamba, 2,800 m, 7°55′S, 77°10′W, *Hamilton & Holligan 1411* (S, UC).

VENEZUELA, LARA: Las Sabanetas, above Los Aposentos, 2,530 m, *Steyermark 55311* (F, MO, NY, VEN). MÉRIDA: La Carbonera, 2,200 m, *Aristeguieta 2478* (F, MER, NY, US, VEN); Pico El Aguila, Carretera Chachopo, 3,600 m, *Badillo 5176* (MY); Páramo de Los Conejos, 3,500 m, *Bernardi 1257* (MER, NY); Páramo de Mucuchies, 3,750 m, *Humbert 26304* (P, RSA, US); Laguna Mucubaji, 3,650 m, *Steyermark 57508* (F). TÁCHIRA: Cabeceras del Río Quinimarí, 15 km S de San Vicente de La Revancha, 2,400 m, *Steyermark et al. 100637* (VEN); Quebrada Agua Azul, 14 km SE de Delicias, 2,300 m, 7°31′N, 72°24′W, *Steyermark & Liesner 118373* (MO, VEN). TRUJILLO: Near Guirigay, 3,300 m, *Aristeguieta & Medina 3647* (NY, VEN); Dist. Boconó, Páramo de Tuñame, 3,120 m, *Berry 3122* (MO); Entre La Peña y Agua del Obispo, 28–34 km de Carache, 2,400 m, *Steyermark 104954* (M, S, VEN). ZULIA: Dist. Perijá, Serrania de Los Motilones, 10°00′N, 72°58′W, *Tillett & Honig 747-834* (MO); Dist. Maracaibo, Serrania de Valledupar, 3,100 m, 10°25′N, 72°52′W, *Tillett 747-1132* (MO).

Epilobium denticulatum is a common, widespread, highly variable species that has its primary distribution throughout the northern and central Andes. It may be distinguished from other closely related species by its nodding inflorescence, bluish or lavender staminal filaments, leaves with relatively few denticulate teeth, and strongly appressed, or more rarely, slightly spreading, minute blunt-tipped hairs on the surfaces of the leaf blades. This latter feature and colored staminal filaments are shared with *E. pedicellare*, but they are unknown in any other species. *Epilobium pedicellare* is immediately separable, however, by its alternate serrate leaves and erect inflorescences.

There are two other sympatric species, *E. fragile* and *E. ciliatum*, with which some plants of *E. denticulatum* might be confused. *Epilobium fragile* differs in its densely caespitose habit, thin wiry stems mostly less than 10 cm tall, sparse

pubescence, and few flowers. Some plants of *E. denticulatum* approach *E. fragile* in stature, but they generally have larger leaves, denser pubescence, more flowers and the appressed hairs mentioned above. *Epilobium ciliatum* is sympatric in a very limited area at the southern end of the range of *E. denticulatum*, and can be separated immediately by its white flowers, fleshy turions, and longitudinally ridged seeds.

Epilobium denticulatum was the first species described from South America. Its original circumscription and distribution, however, were based on two species, as recognized here, *E. denticulatum* and *E. puberulum*. From the beginning, the name *E. denticulatum* was used for the widespread northern Andean species. Specimens of *E. puberulum* have often been misidentified as *E. denticulatum*. These two species are allopatric, and, while they may be closely related, *E. puberulum* differs significantly in its erect inflorescences, complete lack of glandular hairs, distinct floral morphology, and petal color.

The long persistent confusion concerning the assignment of plants to the various taxa surrounding *Epilobium denticulatum* is well illustrated by the problems encountered by Haussknecht (1884). He recognized seven species in his group Denticulatae, one of which is a synonym of *E. pedicellare*. A careful reexamination of the specimens he used showed that five of the remaining six species are heterogeneous, containing components from two or more species. Thus, his treatments of *E. denticulatum*, *E. meridense*, and *E. caesium* include collections of *E. puberulum* (e.g., Coronel, Arauco Prov., *Ochsenius*, GOET; Hacienda San Juan, Valdivia Prov., *Ochsenius*, BREM; and Quebrada Verde, Valparaiso Prov., *Maximow in 1854*, JE, respectively), while *E. bonplandianum* included specimens of *E. ciliatum* from Mexico and South America (e.g., Cordillera Hurtado, Limarí Prov., Chile, *Gay in 1837*, P). Part of the confusion with this last name is probably due to the fact that the five specimens of *E. denticulatum* cited, including type material of *E. bonplandianum*, are all late season, flowered-out plants that are superficially very similar to some specimens of *E. ciliatum*. *Epilobium repens* was described from specimens from Volcán Orizaba, Mexico, that are referable to *E. ciliatum* (Hoch, 1978). Haussknecht, however, included four collections of *E. denticulatum* in the specimens cited under that species. Superficially, the Mexican specimens are similar to those of *E. denticulatum* from South America in stature, loose innovations, and the nodding inflorescences, but are distinguishable by other features. Although Haussknecht was a very astute observer of epilobiums and had a broad understanding of them on a world wide basis, the species that he included in his Denticulatae were apparently very troublesome to him. His *Monographie* (Haussknecht, 1884) formed the source for the report of *E. denticulatum*, *E. bonplandianum*, *E. caesium*, and *E. meridense* in the Flora de Chile (Reiche, 1898).

The most recent treatment, and the only subsequent work of any consequence, for *Epilobium denticulatum* is that of Samuelsson (1923). He recognized ten species and five varieties in this complex, of which six species and four varieties were proposed as new. Many of his new taxa were based on unique morphological types, which because of the relatively few collections available to him seemed amply distinct, e.g., *E. hirtum*, *E. bolivianum*. It is interesting to note that even though Samuelsson described a large number of new taxa, he discussed in several

places the difficulty of separating the species and their polymorphic nature (Samuelsson, 1923; p. 251, 255, 257). In a later publication (Samuelsson, 1930), he rejected two of these new species, *E. andicolum* and *E. asplundii*, considering them to be robust variants of *E. denticulatum*, and synonymized *E. denticulatum* var. *aberans* with *E. meridense* var. *helodes*. In delimiting most of his taxa, Samuelsson placed great emphasis on the density and distribution of pubescence, especially on the ovaries, pedicel length, and flower size, all of which are relatively variable characters.

Patterns of morphological variation within *E. denticulatum*, as circumscribed here, are extremely reticulate and diverse, and reflect the variety of selection pressures encountered throughout its enormous range. The same types of morphological features appear numerous times throughout its range, with some geographic differentiation. Superimposed on these patterns is variation because of elevational and microclimatic conditions, as well as interpopulational differences related to the high degree of autogamy and consequent fixation of certain characters.

The size, habit and branching patterns of *E. denticulatum* are extremely variable and are strongly influenced by exposure or elevation. The smallest plants are often found at higher elevations or in open or drier sorts of places. At these same elevations, however, much more robust plants can usually be found in more sheltered areas. There is also a pattern of increasing size at lower elevations. Most plants that exceed 80 cm in height come from areas below 3,000 m. Branching patterns are dependent on elevation and microclimate, but also on the age of the plants. Often stems are simple or with a few branches. As the plant ages, they may branch profusely or not at all. This feature is highly variable within populations and shows no geographic correlation. Many times, older stems that have nearly completed flowering may lose the nodding aspect of the inflorescence and appear erect.

Leaf size and, to a lesser extent, shape vary considerably and usually in parallel with the size of the plants, the smaller leaves on small plants, and larger ones on large plants. There are sporadic collections of extremely small-leaved plants from a number of different localities.

Similarly, large-leaved, usually more robust plants are also found throughout the range of the species with increasing frequency in southern Peru, Bolivia, and Argentina (e.g., Between Trujillo and Boconó, Edo. Trujillo, Venezuela, *Alston 6503*, BM; Entre Las Vegas y La Ribera, Dpto. Valle, Colombia, *Cuatrecasas 20430*, F, RSA; Chihuata, Dpto. Arequipa, Perú, *López & Miranda 5530*, RSA; Near La Cumbre, Dpto. La Paz, Bolivia, *Solomon 5013*, MO; Infiernillo, Tucumán Prov., Argentina, *Hjerting et al. 9457*, C). Plants of this type formed the basis for the names *E. andicolum* and *E. asplundii*.

Plants with very large leaves (greater than 5 cm) are found only in the altiplano and again in the Sierra Grande de Córdoba. Throughout the altiplano and southward in San Juan and Mendoza provinces, Argentina, there is a mixture of small and large-leaved plants, often within the same population. The populations from the Sierra Grande de Córdoba consist of predominantly large-leaved and usually robust plants. This pattern is modally different from that found in the rest of the range of *E. denticulatum* but is most likely the result of the derivation of the

Sierra Grande populations from more or less large-leaved plants from the southern altiplano to the west and northwest by long-distance dispersal.

The primary leaf shape in *E. denticulatum* is lanceolate, with acute apices. Rarely individuals may have nearly ovate leaves with subcordate bases (e.g., La Cumbre, Dpto. La Paz, Bolivia, *Asplund 4014,* the type of *E. bolivianum*; Nevado del Ruiz, Dpto. Caldas-Tolima, Colombia, *Barclay & Juajibioy 6380,* RSA; Calca, Dpto. Cuzco, Perú, *Hammerlund 620,* S). More frequently the larger-leaved plants mentioned above have somewhat elongate apices, so that the leaves are markedly acuminate.

Pubescence density and distribution is also extremely variable. In general, the upper stems and ovaries are strigillose with an admixture of appressed or slightly spreading glandular or blunt-tipped hairs. These hairs also occur on the surfaces of the leaves, a feature shared only with *E. pedicellare*. Often the leaves become glabrate as they mature, so that only a few or none of the appressed hairs are found on the surfaces of older leaves. Density of both hair types is highly variable throughout the range of the species, although there is a trend toward denser, almost canescent, strigillose pubescence in the southern páramos and altiplano. The increased pubescence may in part be due to the drier atmospheric conditions found throughout much of the altiplano, in contrast to the moist páramos found in Costa Rica, Venezuela, and Colombia, where this pubescence type is not common.

The most striking qualitative difference in pubescence type seen in *E. denticulatum* is the erect or spreading hirsute hairs that characterize plants that have gone under the name *E. hirtum* (e.g., Pichupichu, Dpto. Arequipa, Perú, *Sandeman 3758*; Chuquibamba, Dpto. Arequipa, Perú, *Stafford 1165*; La Paz, Bolivia, *Buchtien 531*; Socoroma, Tarapacá Prov., Chile, *Ricardi et al. 190*). The distribution of this character is limited to the vicinity of La Paz, Bolivia, Arequipa, Perú, and a single collection from Tarapacá Prov., Chile. In addition to the transformation of strigillose hairs to longer erect ones, the usually appressed glandular hairs of the leaves, stems, and ovaries are also erect and longer than normal.

Epilobium hirtum was originally described from robust, fairly large-leaved plants from La Paz, Bolivia. Except for pubescence, most of these plants are indistinguishable from those called *E. andicolum* (e.g., Ollantaitambo, Dpto. Cuzco, Perú, *Pennell 13670*). Mixed populations of plants with appressed and erect pubescence are indistinguishable except on the basis of the hair type (e.g., Río Chili, Arequipa, Dpto. Arequipa, Perú, *Munz 15511*). The hirsute pubescence gives the plants such a distinctive appearance that those with this feature are immediately identified as *E. hirtum*. This is an excellent example of the artificial separation of plants into different taxa based on a single character in a highly polymorphic group.

Flowers in *E. denticulatum* vary considerably in size, but exhibit no geographic patterns in their size distribution. Plants with very large flowers or very small ones are found throughout the range of the species, although the majority have petals of intermediate size. Even within populations flower size can be variable, with mixtures of large and small flowered plants (e.g., La Oroya, Dpto. Junín, Perú, *Kalenborn 19*; and Araranca, Dpto. Puno, Perú, *Pennell 13432*).

At anthesis most flowers, as well as the inflorescence, as a whole nod. In smaller flowers the anthers of the longer stamens, and often the shorter, usually

dehisce directly on the stigma, sometimes even before the flower fully opens. In larger flowers, the stamens are normally held away from the stigma at anthesis. After several hours, the longest bend inward, shedding their pollen on the stigma. Only rarely is the stigma completely exserted (Valle Paucartambo, Dpto. Cuzco, Perú, Herrera 3358, F); more frequently in the larger flowers, the stigma is partially exserted, but the longest stamens are able to reach at least the lower portion of the stigma, so some measure of self-pollination can take place (e.g., Ollantaitambo, Dpto. Cuzco, Perú, *Pennell 13670,* PH, GH, F, NY; Huanta, Dpto. Ayacucho, Perú, *Weberbauer 7505,* F, GH, NY, US). On cloudy or rainy days even the largest flowers may open only partially, or not at all, making them functionally cleistogamous.

Epilobium denticulatum is sympatric with at least *E. pedicellare, E. hirtigerum, E. glaucum,* and *E. ciliatum,* and presumably also with *E. fragile.* The geographic ranges of both *E. pedicellare* and *E. fragile* are completely contained within that of *E. denticulatum. Epilobium denticulatum* is sympatric with *E. hirtigerum* only in the Sierra Grande de Córdoba and with *E. ciliatum* in this same mountain range, and also in the Sierra de San Luis and in a narrow band in southern San Juan and eastern Mendoza Province, Argentina. *Epilobium glaucum* overlaps with *E. denticulatum* only in this last named area.

Natural hybridization involving *E. denticulatum* and any of these other species is apparently relatively rare. Several hybrids have been reported involving *E. pedicellare* (Samuelsson, 1923, 1930), but it is believed that all except one were based on non-hybrid specimens of *E. pedicellare* (q.v. for discussion), although hybrids of this combination would be very difficult to distinguish. Two specimens of what are possibly hybrids between *E. denticulatum* and *E. ciliatum* have been seen (Copina, Sierra Grande, Córdoba Prov., Argentina, *Grassi 2280,* LIL; and in the vicinity of Mendoza, Mendoza Prov., Argentina, *Carette in 1906,* BA). Both have intermediate leaf shape, appressed hairs on the leaf surfaces, strongly reduced seed set, and pollen stainability of 27% and 23% respectively. Although *E. denticulatum* and *E. ciliatum* both have the same chromosome arrangement, AA, the depressed pollen stainability is not unusual. Artificial hybrids between these species had pollen stainability in the range of 37–65%.

The relationship of *E. fragile* with *E. denticulatum* is not clear (see discussion of *E. fragile*). There are several collections from northern Argentina and Chile (Río Despensas, Dpto. Humahuaca, Jujuy Prov., Argentina, *Ruthsatz IV-60,* MO; Río Despensas, Dpto. Cochimoca, Jujuy Prov., Argentina, *Boelcke et al. 770,* BAA; Km 99, camino Arica-Chapiquiña, Tarapacá Prov., Chile, *Marticorena et al. 59,* MO, CONC; Camino de Huara a Cancosa, al interior de Coscaya, Tarapacá Prov., Chile, *Richardi et al. 418,* MO, CONC) that approach *E. fragile.* They are tentatively retained in *E. denticulatum* because of their larger size, dense strigillose pubescence, and appressed hairs on the leaf surfaces. These plants will deserve careful reconsideration when more material becomes available from these poorly explored regions.

2. **Epilobium pedicellare** Presl, Reliquiae Haenkeanae 2:30. 1831. TYPE: "Chile," without specific locality, 1790, *T. Haenke* (PR-495768, holotype, photograph MO). Probably collected in Perú, and the label information is in error.

E. haenkeanum Hausskn., Oesterr. Bot. Z. 29:118. 1879. TYPE: Perú, without specific locality, 1790,

T. Haenke (PR, holotype, photograph MO, fragment JE). Hausskn., Monogr. *Epilobium* 268, *tab. 16, f. 72, 72a*. 1884. H. Lév., Iconogr. *Epilobium, tab. 208*. 1911. Samuelsson, Svensk Bot. Tidskr. 17:262. 1923. MacBride, Field Mus. Nat. Hist., Bot. Ser. 8(4):532. 1941.

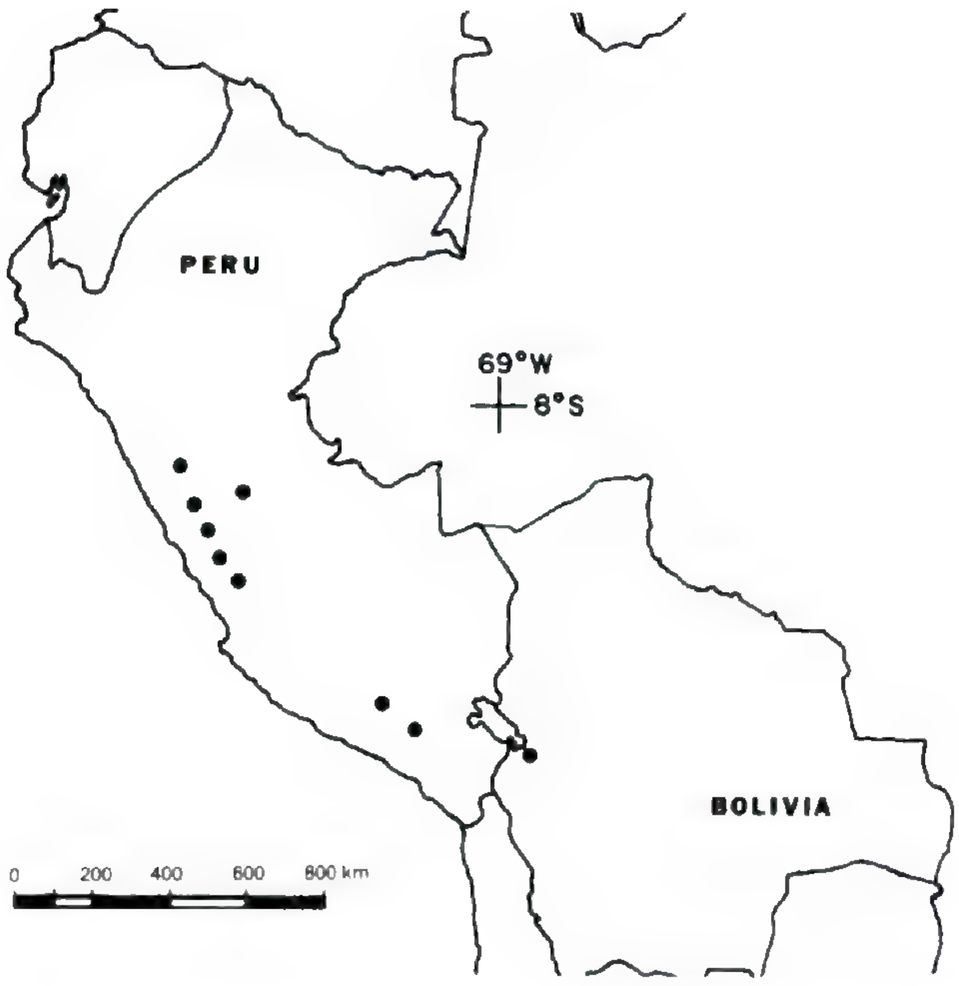
E. peruvianum Hausskn., Monogr. *Epilobium* 263. 884. TYPE: Perú, Dpto. Lima, "ditches and Río Rimac, near Lima," *W. Nation* (K, holotype, photograph MO). H. Lév., Iconogr. *Epilobium, tab. 210*. 1911.

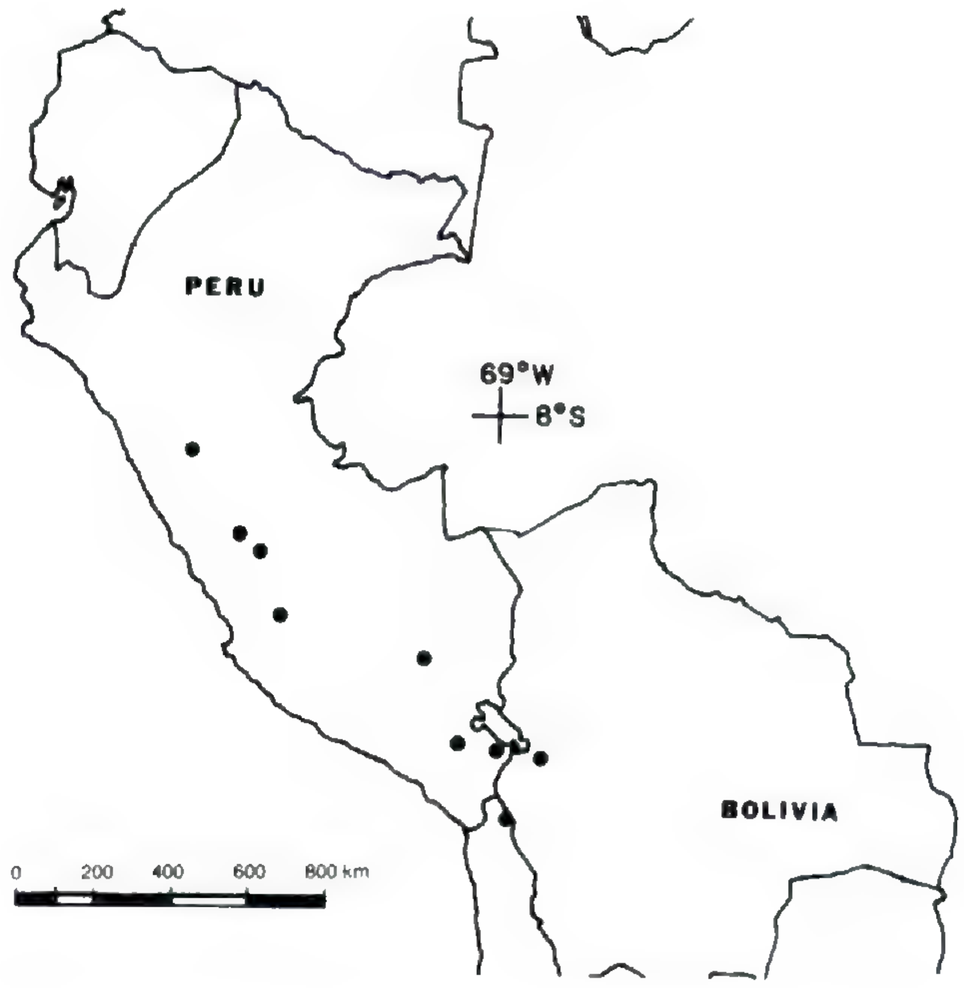
Robust perennial herb, the stems (30–)40–120 cm long, reproducing vegetatively by elongate leafy shoots from near the base. Stems decumbent to pendent, or ascendent, sparsely branched above, usually with an abrupt bend leading to the erect inflorescence, thick, hollow, lustrous reddish brown, strigillose all around the stem in the inflorescence, below pubescence restricted to raised descending lines from the decurrent petiole bases. Leaves mostly alternate, opposite only on young shoots or near the base, thin, dark green, narrowly ovate to ovate, 1.2–4.3(–5) cm long, 0.5–1.4(–1.8) cm wide, acute to acuminate, rarely obtuse at the apex, finely serrate or doubly serrate with (7–)16–30(–43) irregularly sized teeth on each side, acute to cuneate at the base, sparsely strigillose on the margins and the abaxial midrib, both surfaces with appressed blunt-tipped or glandular hairs, 0.05–0.1 mm long, lateral veins prominent beneath, 3–4(–5) on each side of the midrib, on petioles 1–3(–4) mm long, rarely sessile. Inflorescence erect, simple, the flowers congested at anthesis, the internodes elongating somewhat in fruit. Flowers erect. Ovaries often reddish, strigillose, sometimes densely so, usually with scattered appressed glandular hairs, 0.7–1.5 cm long, on pedicels 0–1 mm long. Floral tube often reddish purple, 1.1–1.5 mm deep, 1.7–2.4 mm across, externally strigillose with scattered appressed glandular hairs, internally glabrous or with a few erect villous hairs, 0.1–0.15 mm long, in a ring near the base. Sepals often reddish purple, lanceolate, 2.5–3.4 mm long, 1.0–1.3 mm wide, strigillose with scattered appressed glandular hairs. Petals pale pink to rose purple, obovate, 3.5–5.5 mm long, 1.7–2.5 mm wide, the notch 0.9–1.3 mm deep. Anthers cream, 0.6–0.9 mm long, 0.4–0.6 mm wide; filaments bluish purple to pale lavender, those of the longer stamens 1.7–2.6 mm long, those of the shorter 0.7–1.8 mm long, the longer, and often the shorter, stamens shedding directly on the stigma at anthesis. Style white, 2.4–3.1 mm long; stigma white, clavate, 1.0–1.4 mm long, 0.6–0.8 mm thick. Capsules erect, with scattered strigillose hairs, 3.1–4.8 cm long, 1.1–1.5 mm thick, on pedicels 0.3–1.5(–2.5) cm long. Seeds brown, papillose, obovoid, 0.8–1.0 mm long, 0.3–0.4 mm thick, the chalazal end with a short appendage 0.04–0.08 mm long, 0.08–0.12 mm wide; coma white, 4.5–7 mm long, readily detaching. Gametic chromosome number, $n = 18$.

Distribution (Fig. 2): On moist stream embankments or seeps, widely scattered in the altiplano of central and southern Perú and western Bolivia at elevations of 2,400–3,600 m. Flowering throughout the year, but perhaps with reduced flowering from June through August, the coolest, driest months.

Specimens examined: BOLIVIA, LA PAZ: Prov. Murillo, La Paz, *Asplund 58* (UPS); *Bang 75a* (NY, PH, US); *Buchtien in 1907* (C, F, US), *in 1910* (BAF, E, F, GB, GH, JE, L, NY, UPS, Z), *in 1910* (BM), *in 1912* (K), *in 1913* (C, JE, LD, MO, S, UPS), *in 1921* (GH), *8431* (US), *8433* (B, BM, BR, C, E, G, K, M, MO, S); *Pennell 14217* (F, GH, NY, PH); *Rusby 1806 (April 1885)* (NY, WIS), *1806 (Oct. 1885)* (F, GH, MICH, NY, PH, US); *Shepard 157* (CAS, GH, NY, P); *Solomon 5147* (MO); *Thuegsegges & Feurer 4098* (MO); *Weddell in 1851* (JE, P).

PERÚ, Without locality, *MacLean* (K); *Neé in 1790* (F, MA). ANCASH: Prov. Cajatambo, Ocros, 3,400 m, 10°24′S, 77°24′W, *Weberbauer 2706* (G, UPS). AREQUIPA: Arequipa, Río Chili, *Averett 1007B*





FIGURES 2–3.—2. Distribution of *Epilobium pedicellare*.—3. Distribution of *Epilobium fragile*.

(MO); Harvard Observatory, *Castle in 1911* (GH); without locality, *Harrison in 1896* (GH); Prov. Cailloma, Chivay, 3,500 m, 15°38′S, 71°36′W, *Mueller et al. 2134* (LZ). HUANUCO: Tambo de Vaca, 9°42′S, 75°47′W, *Martinet 168* (P). JUNÍN: Abocongo, *Infantes 160* (LIL). LIMA: Prov. Huarochirí, Viso, 2,700 m, *Asplund 11137* (S); Prov. Yauyos, Tupe, 2,950 m, 12°40′S, 75°46′W, *Cerrate 1116* (MO); Prov. Huarochirí, Picoy arriba de Surco, 3,200 m, 11°52′S, 76°28′W, *Ferreyra 6086* (MO, US, USM); Prov. Canta, entre Huascoy y Cormo, 3,000 m, 11°25′S, 76°45′W, *Ferreyra 18405* (MO); Matucana, *MacBride & Featherstone 90* (F, G, GH, S, US); *Martinet* (P); Río Chillón, Km 123 on road Canta-Culluhuay, *Mueller et al.* (LZ); Río Chillón, Obrajillo, 11°54′S, 77°09′W, *Pennell 14384* (PH); Río Huaura, 11°06′S, 77°39′W, *Ruiz & Pavón in 1778* (P).

Epilobium pedicellare is easily distinguished from the other South American species by its mostly alternate, finely serrate leaves, the teeth of uneven size, thick hollow stems, and an erect, congested inflorescence at least in early flowering. Only *E. hirtigerum* from eastern South America and the introduced *E. paniculatum* have mostly alternate leaves, but their ranges are widely separated from that of *E. pedicellare*, which is confined to the altiplano of Perú and Bolivia.

Presl originally described this species from a specimen collected by T. Haenke during the Malaspina Expedition (1789–1793). The herbarium sheet at Prague (PR) is labeled as coming from Chile, although this species is not known to grow within Chile as it was constituted in 1790, nor did Haenke collect in northern Chile, the only areas where *E. pedicellare* might be found (Kühnel, 1960). Undoubtedly the plant is mislabeled and probably came from Perú, since the many collections from the Malaspina Expedition are notorious for their incorrect labels (cf. Hitchcock, 1909).

Shortly after the appearance of *Reliquiae Haenkeanae*, Hooker & Arnott (1833) used the name *Epilobium pedicellare* to which they referred several Chilean and Argentinean collections of John Gillies. These proved to be a mixture of *E. denticulatum*, *E. ciliatum*, and *E. glaucum*, thus obscuring the identity of *E. pedicellare* early on.

The next botanist who dealt with any material referable to *E. pedicellare* was Haussknecht, who described *E. haenkeanum*, also from a Haenke specimen at

Prague (PR), but not the same one used by Presl (Haussknecht, 1879). Apparently Haussknecht never saw the type of *E. pedicellare*, although his annotations are found on a number of other specimens from Presl's herbarium. As a result, in the preparation of his *Monographie*, Haussknecht was uncertain as to the exact identity of *E. pedicellare* and tentatively assigned it as a synonym of *E. denticulatum* (Haussknecht, 1884).

To confuse the issue further, the type of *Epilobium haenkeanum*, at the time Haussknecht described it, was annotated as *E. denticulatum* with reference to Presl's brief description of that species in *Reliquiae Haenkeanae* (Presl, 1831). This description, however, differs substantially from the characters exhibited by the specimen. Haussknecht (1884) pointed out this discrepancy and provisionally placed Presl's description of *E. denticulatum* with his *E. caesium* without having seen the specimen from which Presl drew the description. Among the extant specimens at Prague (PR), there is a single sheet annotated as *E. denticulatum* in the same hand as the label for *E. pedicellare*, presumably that of Presl. This specimen is a small piece of a probable hybrid between *E. ciliatum* and *E. glaucum*, which matches the description of *E. denticulatum* as given by Presl and is probably the one on which it was based. Unfortunately, this specimen is labeled as coming from Chile, not Perú, as given in *Reliquiae Haenkeanae*, so some doubt still remains.

In his *Monographie*, Haussknecht (1884) also described a third taxon referable to *Epilobium pedicellare* as *E. peruvianum*, which he allied with *E. franciscanum* Barbey (*E. ciliatum* subsp. *watsonii* (Barbey) Hoch & Raven) to which it bears a vague resemblance but is not directly related.

As a result of Haussknecht's interpretation of *E. pedicellare* and the difficult access to Presl's material, subsequent authors have used the name *E. haenkeanum*, with *E. pedicellare* considered as a synonym of *E. denticulatum*.

Epilobium pedicellare has been relatively rarely collected and is apparently much more scattered in its distribution than the widespread *E. denticulatum* with which it often grows. This may be due to some ecological specialization because the only habitats where this species has been seen are very steep, almost vertical seeps that are continuously wet. In contrast, *E. denticulatum* is much more weedy, growing in ditches, seeps, stream banks, or almost any habitat that has a permanent supply of water. In places where *E. pedicellare* is found, it often grows in a pendent or reclining fashion with an abrupt U-shaped bend before the beginning of the erect inflorescence. The stems are often more than 1 m long and form dense masses. This unusual habit can often be seen on herbarium material and is very different from the ascending or erect stems and nodding inflorescences of *E. denticulatum*.

The nearest relative of *E. pedicellare* is probably *E. denticulatum*, with which it shares two unique characters, unknown in any other South American species: the presence of minute appressed or slightly spreading blunt-tipped hairs, usually on both surfaces of the leaves, and pale lavender to bluish staminal filaments.

Because the range of *Epilobium pedicellare* is completely contained in that of *E. denticulatum* and they often grow together, it would seem likely that hybrids would occasionally be produced. Samuelsson (1923, 1930) reported a number of plants as hybrids, but only one specimen of these seems likely to be of truly

hybrid origin (La Paz, Dpto. La Paz, Bolivia, *Buchtien 37*, US, mixed with *E. pedicellare*). The others fall within the variation seen in *E. pedicellare*, although hybrids of this combination are very difficult to distinguish. Based on the morphology of the two putative parents, the specimen indicated above is intermediate with leaves having fewer, less sharp teeth, thinner stems, and larger flowers than is typical for *E. pedicellare*. This specimen had a pollen stainability of 81%.

3. Epilobium fragile Samuelsson, Svensk Bot. Tidskr. 17:291, *tab. 4, f. 3a–c.* 1923. TYPE: Bolivia, Dpto. La Paz, Prov. Murillo, "in rupibus irrigatis," La Cumbre, 4,500 m, 26 May 1921, *E. Asplund 4015* (UPS, lectotype, photograph MO; B (destroyed, photographs BH, MO, US), LD, S, W, Z, isolectotypes). Samuelsson, Svensk Bot. Tidskr. 24:7. 1930. MacBride, Field Mus. Nat. Hist., Bot. Ser. 8(4):531. 1941.

E. nivale auct. non Meyen: Samuelsson, Svensk Bot. Tidskr. 17:290. 1923, pro parte; MacBride, Field Mus. Nat. Hist., Bot. Ser. 8(4):532. 1941.

Low, densely caespitose perennial herb, 3–10(–15) cm tall. Stems many, thin, usually reddish brown, decumbent or erect, mostly simple or few-branched from a fibrous, or somewhat woody rootstock, subglabrous, with a few strigillose hairs, 0.1–0.2 mm long, at the petiole bases, or occasionally scattered in descending lines from the petiole bases, rarely with a few erect glandular hairs, 0.1–0.2 mm long. Leaves all opposite or alternate in the inflorescence, thick, occasionally reddish purple, narrowly ovate to elliptic, rarely lanceolate, 0.4–1.2 cm long, 1.5–4 mm wide, obtuse to rounded, rarely acute at the apex, subentire with 0–3 obscure teeth on each side, acute to cuneate at the base, glabrous, or with a few scattered strigillose hairs on the margins, lateral veins obscure, none or 1–2 on each side of the midrib, on poorly defined petioles, 0–2.5 mm long. Inflorescence erect, simple, few-flowered. Flowers erect at anthesis. Ovaries reddish purple, 0.4–1 cm long, glabrous, or with a few strigillose or erect glandular hairs, on pedicels 1–9 mm long. Floral tube often reddish purple, 0.8–1.2 mm deep, 1.1–2.4 mm across, externally glabrous or with a few strigillose or erect glandular hairs, internally with a sparse ring of a few erect villous hairs, 0.08–0.13 mm long, near the base. Sepals often reddish purple, lanceolate, 2.5–3.3 mm long, 1.1–1.4 mm wide, glabrous. Petals pink to white, obovate, 3.0–5.5 mm long, 1.9–3 mm wide, the notch 0.4–1 mm deep. Anthers 0.6–0.8 mm long, 0.5–0.7 mm wide; filaments of the longer stamens 1.2–3 mm long, those of the shorter 0.7–2 mm long, at least the longer, and usually the shorter, shedding directly on the stigma. Style 1.7–2.6 mm long; stigma subcapitate, 0.8–1.2 mm long, 0.5–1.1 mm thick. Capsules erect, glabrous, 1.8–2.3 cm long, 1.1–1.5 mm thick, on pedicels 2–5 mm long. Seeds pale brown, minutely papillose, obovoid, 1.2–1.3 mm long, 0.4–0.5 mm thick, the chalazal appendage 0.04–0.08 mm long, 0.08–0.12 mm wide; coma pale yellow brown, 3.5–5 mm long.

Distribution (Fig. 3): Typically inhabiting moist crevices in rock outcrops or cliff faces; scattered throughout the Altiplano of Perú, from Dpto. Ancash south to western Bolivia and extreme northeastern Chile at elevations of 4,400–5,000 m. Flowering specimens have been collected from May, June, July and November.

Specimens examined: BOLIVIA, LA PAZ: Ravín de Chuquiaguillo, *Weddell in 1851* (P).

CHILE, I REGIÓN (TARAPACÁ): Parinacota, Lago Cotacotani, 4,500 m, 18°12′S, 69°15′W, *Sudzuki 480* (K).

PERU, ANCASH: Huaraz, 4,600 m, *Weberbauer 2969* (G). CUZCO: Ausangate, 4,800 m, *Rauh-Hirsch P1258* (RSA). HUANCAVELICA: San José de Acobambilla, Nahuincocha, 12°40′S, 75°22′W, *Lloyd & Marshall 100* (K). JUNÍN: La Oroya, 35 km W of Hacienda Cochas, 5,000 m, *Gutte 3256* (LZ); Casa Cancha, Cerro La Viuda, 4,400 m, 11°05′S, 76°35′W, *Wilkes (U.S. Exploring Expedition) in 1839* (GH, K, US). LIMA: Prov. Huarochiri, Casapalca, 4,700 m, *MacBride & Featherstone 867* (F, GH, S, US). PUNO: Caccachara, 80 km SW of Ilave, 4,900 m, *Pearson 107* (PH); San Antonio de Esquilache, 4,500 m, 16°06′S, 70°18′W, *Stafford 729* (BM, F), *Tutin 1181* (BM).

Epilobium fragile is a diminutive, high Andean species that has been collected rarely, so little is known of its biology or relationships. It forms low, densely caespitose clumps, with the thin, wiry stems seldom more than 10 cm long. Plants are characteristically glabrous, except for a few strigillose hairs on the leaf margins, at the junction of the fused petiole bases, and rarely in scattered, descending lines, with or without a few scattered erect glandular hairs.

Epilobium fragile has usually been confused with *E. nivale,* even by Samuelsson, who described the former (Samuelsson, 1923). As a result, *E. nivale* has been erroneously reported from Peru (MacBride, 1941, and Samuelsson, 1923). Samuelsson considered *E. fragile* to be most closely related to *E. nivale,* both of which he segregated in his group Nivalia, based on their compact growth form, small leaves, and the more or less glabrous nature of the plants (Samuelsson, 1923). Superficially both species are quite similar in habit and overall morphology. However, *E. fragile* differs from *E. nivale* by the presence of strigillose and glandular hairs, thin, wiry stems, ovate to elliptic, blunt-tipped leaves, and slightly larger, often white flowers, although there is some overlap in all the characters except pubescence. Ecologically they are also separated, with *E. fragile* growing in crevices in rocks, and *E. nivale* inhabiting moist places near bogs or along streams. The present ranges of *E. fragile* and *E. nivale* are separated by about 1,500 km. Additional exploration of the Andes in northern Chile and northwestern Argentina, however, may expand the range of both species.

The chromosomal arrangement of *E. fragile* is unknown, so the possibility that it may be more closely related to *E. nivale,* which has the BB arrangement cannot be ruled out. A second, and what is considered more likely, hypothesis is that *E. fragile* is most closely allied to *E. denticulatum,* a species with the AA chromosomal arrangement, which is widespread in the northern and central Andes. In addition to having strigillose and glandular hairs in common, some of the smaller specimens of *E. denticulatum* approach *E. fragile* in habit, although they are larger, more densely pubescent, and usually have more and larger flowers. The geographic range of *E. fragile* is completely contained in that of *E. denticulatum,* and, considering the very recent nature of the high montane habitats where *E. fragile* is found, it may have been derived directly from *E. denticulatum.*

4. **Epilobium puberulum** Hook. & Arn., Hook. Bot. Misc. 3:309. 1833. TYPE: Chile, X Región (Los Lagos), Prov. Chiloé, Isla Chiloé, 1831, *H. Cuming 36* (K, lectotype here designated, photograph MO; BM, BP, BR (probable), E 2 sheets (photographs A, K), GH, OXF (probable), PRC, TCD, W (photographs BH, GH, MO), isolectotypes). Hausskn., Monogr. *Epilobium* 257. 1884. Reiche, Fl. Chile 2:245. 1898. H. Lév., Iconogr. *Epilobium tab. 192, 197* (as *E. bar-*

beyanum), *211* (as *E. denticulatum*). 1911. Samuelsson, Svensk Bot. Tidskr. 17:248. 1923.

E. denticulatum Ruiz & Pavón, Fl. Peruv. et Chil. 3:78. 1802, pro parte, as to plants from Concepción, Chile.

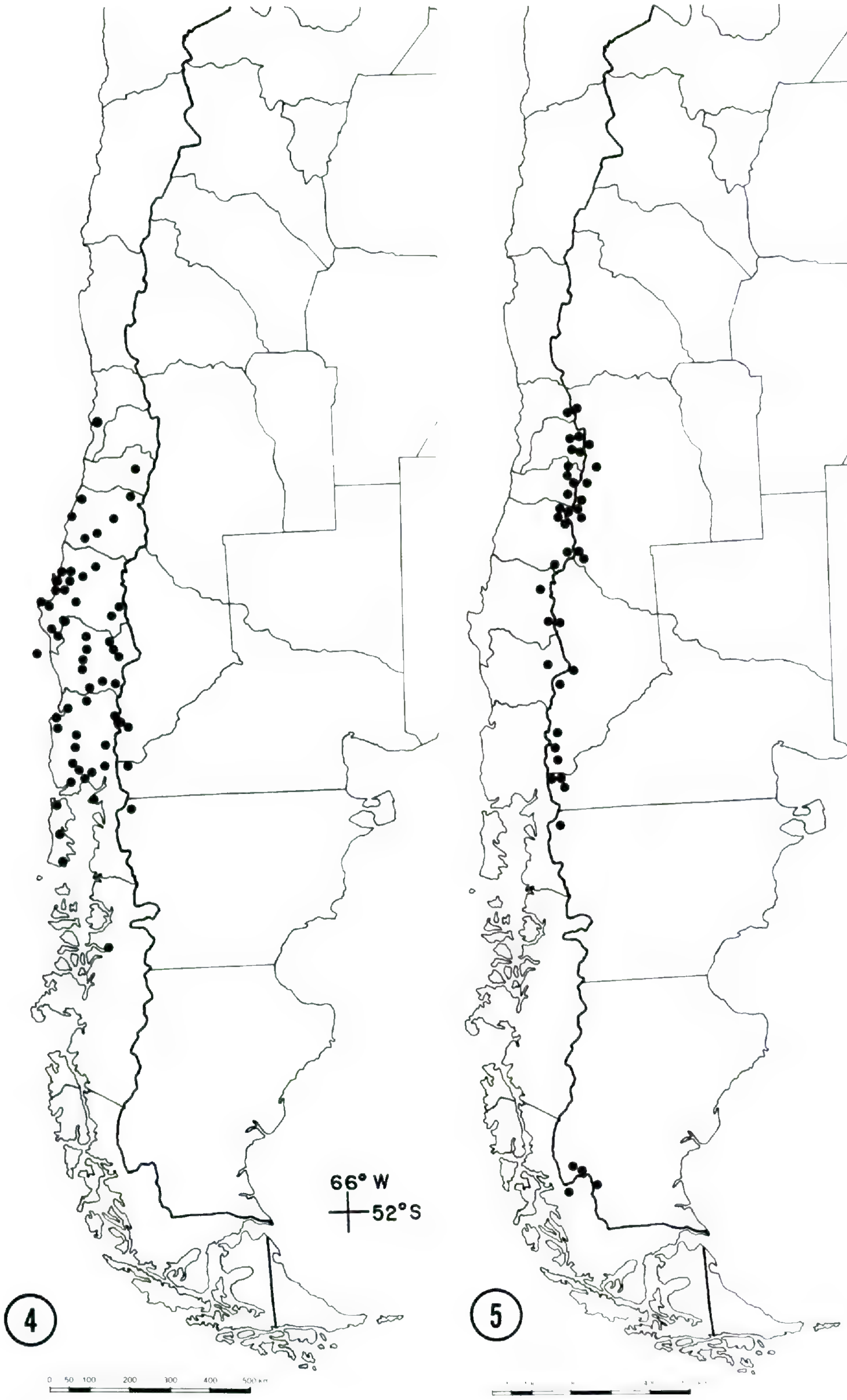
E. denticulatum auct. non Ruiz & Pavón: Gay, Hist. Fis. Chile 2:247. 1846.

E. pedunculatum R. Phil., Anal. Univ. Chile 41:713. 1872. TYPE: Chile, VI Región (O'Higgins), Cordillera de Colchagua, November 1860, *C. Landbeck* (SGO-53114, lectotype here designated, photograph MO; SGO-41459, isolectotype, photographs GH, MO).

E. gracile R. Phil., Anal. Univ. Chile 84:748. 1893, non Bruegg., Jahres-B. Naturf. Ges. Graub. Ser. 2, 25:70. 1882. TYPE: Chile, X Región (Los Lagos), Prov. Valdivia, Cordillera de Valdivia, Pirihuaico, January 1887, *O. Philippi* (SGO-53083, lectotype here designated, photograph MO; SGO-53046, isolectotype, photographs GH, MO).

Perennial herb, 20–60 cm tall, overwintering and reproducing vegetatively by elongate leafy shoots produced at or near the base. Stems erect, usually branched above, and often below, or simple, terete, strigillose to spreading hirsute throughout, the hairs 0.15–0.4 mm long, with obscure raised descending lines from the decurrent petiole bases, these often poorly developed or absent. Leaves mostly opposite, alternate above and in the inflorescence, often with fascicles of small leaves in the axils, thin, bright green, lanceolate to rarely narrowly ovate, 0.8–2.8(–3.3) cm long, 0.2–1(–1.5) cm wide, acuminate to acute at the apex, regularly and remotely denticulate with 3–6 teeth on each side, cuneate to acute, occasionally obtuse or rounded at the base, strigillose to spreading hirsute on both surfaces, usually glabrate with age and then the pubescence restricted to the margin and the abaxial and adaxial midribs and lateral veins, the lateral veins obscure, 2–4 on each side of the midrib, on more or less well defined petioles, 0.5–2 mm long. Inflorescence erect, simple or branched, the leaves subtending the flowers usually reduced in size. Flowers erect. Ovaries often reddish purple, densely strigillose to spreading hirsute, (0.8–)1.2–2.5(–3) cm long, on pedicels 0.4–1.3(–1.7) cm long. Floral tube 1–2 mm deep, 1.4–2.1 mm across, externally strigillose to spreading hirsute, internally with a ring of erect villous hairs, 0.2–0.3 mm long, near the base. Sepals lanceolate, 2–3.1 mm long, 0.9–1.3 mm wide, strigillose to spreading hirsute. Petals clear salmon pink, broadly obovate, 3.5–5 mm long, 2.5–3.2 mm wide, the notch 0.8–1.5 mm deep. Anthers cream to white, 0.6–0.8 mm long, 0.4–0.6 mm wide; filaments cream to white, those of the longer stamens 0.9–1.3 mm long, those of the shorter 0.3–0.6 mm long; only the longer shedding directly on the stigma at anthesis. Style cream to white, 2.1–2.8 mm long; stigma cream to white, clavate, 0.8–1.6 mm long, 0.5–0.8 mm thick. Capsules erect, strigillose or spreading hirsute, (2–)3.2–5(–6.6) cm long, 1–1.4 mm thick, on pedicels 0.5–2 cm long. Seeds brown, papillose, obovoid, 0.7–0.9 mm long, 0.3–0.4 mm thick, the chalazal end with a short appendage 0.04–0.08 mm long, 0.06–0.1 mm wide; coma white, 5–7 mm long. Gametic chromosome number, $n = 18$.

Distribution (Fig. 4): Frequent and somewhat weedy, along roadsides, gravelly or sandy stream beds, embankments, and other open, moist, usually disturbed sites. Widely distributed in central Chile from Valparaíso to Isla Chiloé, and Aisén (probably introduced at the latter). In Argentina, found only in a narrow band along the eastern slopes of the Andes in southern Neuquén, Río Negro, and northeastern Chubut provinces. Typically encountered from near sea level to 800 m, rarely as high as 1,000 m. Flowering October to March.



FIGURES 4–5. Distribution of *Epilobium* species.—4. *E. puberulum*.—5. *E. nivale*.

Representative specimens examined: ARGENTINA, CHUBUT: Cholila, *Crovetto 3084* (SI). NEUQUÉN: San Martín de Los Andes, *Bridarolli 2087* (LP); Hua-Hum, *Dawson & Schwabe 2352* (BAB mixed with *E. ciliatum*); Lago Lácar, Peninsula Pucará, *Dawson & Schwabe 2724* (BAA, BAB, MO). RÍO NEGRO: Bariloche, *Burkart 6026* (RSA), *Maldonado in 1941* (F), *Parodi in 1934* (BAA, MO, S); Cerro Otto, 1,000 m, 41°09′S, 71°23′W, *Hosseus 38* (BAF, CORD); Lago Nahuel Huapi, 770 m, *Ljungner 158* (GB).

CHILE, V REGIÓN (ACONCAGUA): *Valparaíso,* Viña del Mar, Hacienda Las Siete Hermanas, *Bultmann 23523* (CONC); Valparaíso, *Claude-Joseph 3565* (US); Quebrada Verde near Valparaíso, *Maximow in 1854* (JE). VI REGIÓN (O'HIGGINS): *Cachapoal,* Termas de Cauquenes, *Gay 187* (F, P, RJ; mixed with *E. ciliatum*); *Reid* (K mixed with *E. glaucum*). *Colchagua,* without locality, *Philippi* (JE, SGO). VII REGIÓN (MAULE): *Curicó,* Vichuquen, 34°53′S, 72°00′W, *Philippi 627a* (SGO); 5 km above Los Queñes, 760 m, 35°00′S, 70°45′W, *Solomon 4335* (MO). *Linares,* Quinamávida, *Philippi in 1893* (SGO); Linares, *Quezada in 1975* (MO). *Talca,* Cordillera de Talca, El Picazo, *Barros 82* (GH); Constitución, *Reiche in 1890* (SGO). VIII REGIÓN (BÍO-BÍO): *Arauco,* Contulmo, *Behn in 1919* (M); Lanalhue, 37°56′S, 73°17′W, *Claude-Joseph 5980* (US); Arauco, 50 m, *Pennell 12966* (PH); Llico, *Philippi in 1861* (SGO); Boca del Río Tubul y Raqui, *Ricardi in 1949* (CONC); Isla Mocha, Laguna Hermosa, *Weldt-Rodríquez 1166/461* (CONC). *Bío-Bío,* Camino de Bío-Bío a Santa Barbara, Estero Pirquinco, 400 m, 37°49′S, 71°40′W, *Marticorena et al. 1015* (CONC, MO); Cordillera de Antuco, La Cueva, *Philippi in 1882* (G, SGO). *Concepción,* Tomé, Collén, *Junge in 1934* (CONC); Gualqui, *Kuntze in 1892* (NY); Florida, *Merxmüller 24865* (M); Nonguén, near Concepción, *Moore 296* (LA); Coronel, *Ochsenius in 1866* (BR, GOET); Concepción, *Dombey in 1782* (P), *Elliot 148* (BM, E, NY), *Ruiz & Pavón in 1782* (MA). *Ñuble,* Entre Cabrero y Salto del Laja, Fundo Trilahue, 130 m, *Marticorena et al. 855* (CONC); Cuchacucha, *Née in 1793* (MA); Montañas de Chillán, *Philippi* (SGO); Pilmaiquén, 36°40′S, 71°51′W, *Philippi* (G); Bulnes, *Philippi in 1878* (JE, SGO); 8 km E of San Rafael on road to San Ignacio, 36°35′S, 72°45′W, *Solomon 4394* (MO). IX REGIÓN (ARAUCANÍA): *Cautín,* Laguna Lorilón, Fundo Flor, *Behn in 1946* (CONC); Villarrica, *Burger in 1965* (GOET); Freire, *Claude-Joseph 5882* (US); Pemehue, 39°29′S, 72°30′W, *Germain in 1894* (SGO); Truf-Truf, 150 m, 38°44′S, 72°34′W, *Gunckel 16908* (US); Pelún, 38°30′S, 72°20′W, *Lanfurgo in 1885* (SGO); 2 km S of Metrenco, *Moore 310* (LA, MO); Termas de Palguín, 700 m, 39°22′S, 71°45′W, *Solomon 4525* (MO). *Malleco,* Cordillera de Nahuelbuta, Los Alpes, Fundo Solano, *Eyerdam 10296* (F, NY, SGO, UC, US); Curacautín, *Maldonado 39* (L); Curacautín, Río Blanco, *Pennell 12726* (F, GH, NY, PH, SGO); Pidima, Fundo Chequenco, 38°01′S, 72°26′W, *Pfister in 1946* (CONC); 16 km N of Curacautín, 800 m, 38°20′S, 70°50′W, *Solomon 4489* (MO). X REGIÓN (LOS LAGOS): *Chiloé,* Puerto Carmen, Quellón, 43°08′S, 73°46′W, *Marticorena 1766* (CONC); Camino de Caicumeo, *Philippi in 1886* (SGO); 14 km S of Castro, *Weldt-Rodríguez 734-29* (CONC). *Llanquihue,* Colegual, 41°22′S, 73°11′W, *Klenner in 1952* (CONC); Hautrunes-Maullín, *Pfister 289* (CONC); Lago Todos Los Santos, Petrohué, *Stubbe in 1961* (VALD); 5 km N of Puerto Montt, *Wall & Sparre in 1947* (S). *Osorno,* Cuinco, 40°32′S, 73°10′W, *Rudolph in 1933* (VALD); Chuyaca, *Rudolph in 1944* (VALD); 3 km E of Puyehue, 40°40′S, 72°18′W, *Solomon 4596* (MO); Centinela, *Sparre 4399* (S); Osorno, *Wall & Sparre in 1947* (S). *Palena,* Rolecha, 41°55′S, 72°50′W, *Pfister in 1951* (CONC). *Valdivia,* Valdivia, *Buchtien in 1901* (BAF, BM, BREM, E, M, P, S, US); *Lechler 441* (G, GH, GOET, K), *Philippi 514* (BM, BREM, G, GOET, JE, P, UPS); Panguipulli, *Claude-Joseph 2556* (US); Corral, *Gunckel 15424* (GH); 5 km NE of La Unión, *Moore 297* (LA, MO); Hacienda San Juan, 40°15′S, 73°05′W, *Philippi in 1886* (JE, SGO); Cordillera de Ranco, Huahum, *Philippi in 1887* (SGO); Cordillera Pelada, *Philippi in 1889* (JE, SGO). XI REGIÓN (AISÉN): *Aisén,* Aisén, *Andreas 509* (U).

Epilobium puberulum is a distinctive species of south central Chile. Its densely strigillose stems and ovaries with generally small lanceolate, few-toothed leaves, erect habit, and salmon-pink flowers make it easily recognized from all its congeners. In fact, the flower color, unknown in any other species of *Epilobium*, is sufficient to identify living material immediately. Superficially some plants of *E. puberulum* have a strong resemblance to some individuals of *E. denticulatum*. There are, however, a number of striking morphological differences; in addition, these two species are allopatric, with a gap of several hundred kilometers between them at their closest point. *Epilobium puberulum* is much more strict in habit and lacks the glandular hairs and nodding inflorescence of *E. denticulatum*, and the flower color is distinctive.

The nearest relative of *E. puberulum* is probably *E. denticulatum*. *Epilobium*

puberulum may have the same chromosomal arrangement as *E. denticulatum* (AA), although this has not yet been confirmed.

The first collections of *E. puberulum* were made by Ruiz, Pavón, and Dombey, from the vicinity of Concepción, Chile, during their stay there in 1782 and 1783. Because of the similarity of these specimens to collections of *E. denticulatum* from Peru, they were all described under the name *E. denticulatum*. Not until some thirty years later were the Chilean plants recognized as a separate species. In subsequent years, R. A. Philippi published two additional taxa based on trivial variants.

Variation within this species is primarily in the size and density of the leaves and the branching pattern. These have no geographic basis, but are mostly related to the age of the plant and the season in which it was collected. Early season plants tend to be simple with fairly large leaves (mostly up to 2.5 cm), with fascicles of small leaves in their axils. As the growing season progresses, these axillary shoots may elongate, producing densely branched plants. The leaves of the secondary shoots are often smaller than those of the primary branches produced earlier. Pubescence also varies, not only in density but in type. For example, a collection from La Unión, Valdivia Prov., Chile (*Moore 297,* MO) is finely strigillose throughout with mostly glabrate leaves, while one from Vegas Blancas, Malleco Prov., Chile (*Solomon 4459,* MO) is densely spreading hirsute with both surfaces of the leaves pubescent.

Ecologically, *E. puberulum* is distinct from most other species. Although it does grow sympatrically with three species, its distribution is the inverse of the normal pattern. As was indicated earlier, except for *E. hirtigerum* and *E. puberulum,* all the South American species are montane, with a few descending to much lower altitudes at higher latitudes. In contrast, *E. puberulum* grows at lower elevations in the coast range, central valley, and the lower slopes of the Andes in Chile, seldom extending above 1,000 m. Its limited and scattered distribution in Argentina suggests that it is a relatively recent introduction to the eastern slopes of the Andes, perhaps appearing there only with the clearing of the forest land and increased communication across the Andes during the last century. The single collection from Aisén, Chile, is undoubtedly a recent introduction.

The high degree of enforced autogamy mentioned earlier makes hybridization with other species an extremely rare event. With one exception no evidence was seen in any of the populations examined in the field or from herbarium material that would indicate that hybridization takes place, although it is not an absolute impossibility. There is one set of very unusual collections made by Bridges at Valparaíso, Chile during the 1830s (*Bridges 179,* BM, E, K, W), apparently all from the same plant or population, which can only be explained as being of hybrid origin, with *Epilobium ciliatum* as the other likely parent. While the upper inflorescence is very *E. puberulum*-like, the lower leaves are several times longer and broader (4.5 × 2 cm), with many more teeth, than is known in any other collection of *E. puberulum*. The leaves approach a size and shape common for *E. ciliatum,* which also occurs in the same area. The flowers are borne singly in the axils of leaves throughout the length of the simple stems, with the antipetalous staminal filaments ca. 0.5 mm long, as is normal in *E. puberulum*. The average pollen stainability of these plants was 74% (range 67–88%). This unusual set of specimens was

identified by Haussknecht as belonging to *E. caesium*, the type of which came from northern Bolivia.

5. **Epilobium ciliatum** Raf., Med. Repos. II 5:361. 1808. subsp. **ciliatum.** TYPE: Northern Pennsylvania, *C. S. Rafinesque*. No specimens of this species collected by Rafinesque are known. (Only the synonymy for names based on South American material is given; for a complete discussion of North American names see Hoch, 1978.)

E. pedicellare auct. non Presl: Hook. & Arn., Bot. Misc. 3:309. 1833, pro parte.

E. pedicellare β latifolium Walp., Nov. Act. Acad. Caes. Leopold. 19, Suppl. 1:328. 1843. TYPE: Chile, VI Región (O'Higgins), Cordillera de San Fernando, *January–March 1831, F. Meyen* (B, holotype, destroyed). No other authentic material has been seen. Haussknecht places *E. pedicellare β latifolium* as a synonym of *E. chilense* and cites a collection of Meyen from the Cordillera de San Fernando at Berlin (B) (Haussknecht, 1884, p. 272). Based on this placement, the brief description and locality, this variety probably belongs here.

E. tetragonum auct. non L.: Hook. f., Fl. Antarct. 2:270. 1847, pro parte; Fl. N. Z. 1:60. 1853, pro parte, as to the plants from the Falkland Islands.

E. chilense Hausskn., Oesterr. Bot. Z. 29:118. 1879. TYPE: Chile, without specific locality or date (1826–31), *H. Cuming* (W, lectotype here designated, photograph MO; BM, BR, M, OXF, PR 2 sheets, isolectotypes). Hausskn., Monogr. *Epilobium* 272. 1884. Reiche, Fl. Chile 2:249. 1898. H. Lév., Iconogr. *Epilobium, tab. 168*. 1911. Samuelsson, Svensk Bot. Tidskr. 17:269. 1923.

E. cunninghamii Hausskn., Oesterr. Bot. Z. 29:118. 1879. TYPE: Chile, XII Región (Magallanes), Prov. Magallanes, Punta Arenas (Sandy Point), 28 February 1863, *R. Cunningham* (LE, holotype, not seen; K, JE (probable), isotypes). Samuelsson, Svensk Bot. Tidskr. 17:276. 1923.

E. valdiviense Hausskn., Oesterr. Bot. Z. 29:118. 1879. *E. chilense* var. *valdiviense* (Hausskn.) Hoss., Trab. Inst. Bot. Farm., Buenos Aires 33:57. 1915. TYPE: Chile, X Región (Los Lagos), Valdivia, *R. A. Philippi* (W, holotype, photograph MO). Hausskn., Monogr. *Epilobium* 271. 1884. Reiche, Fl. Chile 2:249. 1893. H. Lév., Iconogr. *Epilobium, tab. 166*. 1911. Auct. non Hausskn.: Skottsberg, Kungl. Sv. Vet. Akademiens Handlinger 50(3):42. 1913. Samuelsson, Svensk Bot. Tidskr. 17:272. 1923.

E. bonplandianum auct. non H.B.K.: Hausskn., Monogr. *Epilobium* 267. 1889, pro parte as to the plants from Mexico and Chile. Reiche, Fl. Chile 2:246. 1898.

E. magellanicum R. Phil. & Hausskn. ex Hausskn., Monogr. *Epilobium* 271. 1884. TYPE: Chile, XII Región (Magallanes), Prov. Magallanes, without precise locality, summer 1864–65(?), *R. A. Philippi* (W, lectotype here designated, photograph MO; W, JE, SGO-41443, SGO-53016, W (last 4 probable), isolectotypes). The date is taken from SGO-53016. Reiche, Fl. Chile 2:248. 1898. H. Lév., Iconogr. *Epilobium, tab. 171*. 1911. Samuelsson, Svensk Bot. Tidskr. 17:278. 1923; Svensk Bot. Tidskr. 24:9. 1930.

E. aconcaguinum R. Phil., Anal. Univ. Chile 84:745. 1893. TYPE: Chile, V Región (Aconcagua), Prov. Los Andes, Los Andes, on the banks of the Río Aconcagua, December 1885, *R. A. Philippi* (SGO-53036, lectotype here designated, photographs GH, MO; SGO-53010, isolectotype).

E. albiflorum R. Phil., Anal. Univ. Chile 84:745. 1893. TYPE: Chile, X Región (Los Lagos), Prov. Valdivia, Hacienda San Juan, 40°15′S, 73°05′W, January 1886, *R. A. Philippi* (SGO-53044, lectotype here designated, photograph MO).

E. glandulosum auct. non Lehm. Reiche, Fl. Chile 2:250. 1898.

E. valdiviense var. *alboffii* Macloskie, Rep. Princeton Univ. Exped. Patagonia 8:611. 1905. TYPE: Argentina, Terr. Tierra del Fuego, Ushuaia, *N. Alboff*. No authentic material has been seen. This name was originally published without an indication of rank. The varietal level has been chosen because this was the generally used concept at the time of publication.

E. santa-cruzense Dusén, Kungl. Sv. Vet-Akadis. Arkiv. f. Botanik 7(2):208, *tab. 3, f. 2–4, tab. 7, f. 29–34*. 1907. TYPE: Argentina, Prov. Santa Cruz, upper valley of the Río Santa Cruz, 11 February 1905, *P. Dusén 5842* (S, lectotype here designated, photograph MO; K, SI, UPS, isolectotypes). Samuelsson, Svensk Bot. Tidskr. 17:278. 1923.

E. hookerianum Hausskn. ex Skottsberg, Kungl. Sv. Vet. Akademiens Handlinger 56(5):271. 1916. TYPE: Falkland Islands, East Falkland, between Port Darwin and North Arm, 27 January 1908, *C. Skottsberg 122* (UPS, lectotype here designated, photograph MO; BA, GB, LD, S, SGO, isolectotypes).

E. chilense var. *latifolium* Samuelsson, Svensk Bot. Tidskr. 17:270. 1923. TYPE: Chile, V Región

(Aconcagua), Valparaíso, *T. Bridges* (K, lectotype here designated, photograph MO; G, isolectotype). Based on *E. chilense* f. "*latifolia*" Hausskn., Monogr. *Epilobium* 272. 1884.

E. chilense var. *macrum* Samuelsson, Svensk Bot. Tidskr. 17:271. 1923. TYPE: Chile, V Región (Aconcagua), Prov. Quillota, Campana de Quillota, 1856–57, *Ph. Germain* (W, lectotype here designated, photograph MO; K, SGO-53057, SGO-53098, isolectotypes). Based on *E. chilense* f. "*macra*" Hausskn., Monogr. *Epilobium* 272. 1884.

E. longipes Samuelsson, Svensk Bot. Tidskr. 17:271, *tab. 4, f. 2.* 1923. TYPE: Argentina, Prov. Chubut, Lago Buenos Aires, mouth of Río Fenix, 11 December 1890, *C. Skottsberg 946* (UPS, lectotype here designated, photographs MO, S).

E. argentinum Samuelsson, Svensk Bot. Tidskr. 17:273, *tab. 3, f. 5.* 1923. TYPE: Argentina, Prov. Mendoza, Río Salado Superior, Cajón de Las Aguas Amarillas, 22 January 1893, *F. Kurtz 7621* (JE, lectotype here designated, photographs MO, S).

E. constrictum Samuelsson, Svensk Bot. Tidskr. 17:275, *tab. 4, f. 4.* 1923. TYPE: Argentina, Prov. Santa Cruz, Lago Argentino, Valle del Río Santa Cruz, 19 January 1905, *P. Dusén 5614* (S, lectotype here designated, photographs MO, S; BAF, SI, UPS, isolectotypes).

E. caesiovirens Samuelsson, Svensk Bot. Tidskr. 17:279, *tab. 4, f. 1.* 1923. TYPE: Argentina, Prov. Mendoza, Las Cuevas, Puente del Inca, 2,700–2,800 m, 13 February 1903, *G. O. Malme 2889* (S, lectotype here designated, photograph MO; B (destroyed, photographs BH, MO, US), S, UPS, W, isolectotypes).

E. leiophyton Samuelsson, Svensk Bot. Tidskr. 17:280, *tab. 3, f. 1.* 1923. TYPE: Chile, VII Región (Maule), Cordillera de Curicó, 2,500 m, January 1897, *C. Reiche* (UPS, lectotype here designated, photograph MO; B (destroyed, photographs BH, GH, MO, NY, US), isolectotype).

Variable perennial herbs (5–)20–60(–90) cm tall, overwintering and reproducing vegetatively by fleshy-leaved turions or compact leafy rosettes produced at or below ground level, the leaves of the perennating structures subentire, obovate to depressed obovate, or ovate to depressed ovate, 0.5–1.5 cm long, 0.5–2 cm wide. Stems erect, occasionally ascendent, often well branched from the base or above, or sometimes simple, terete or quadrangular, reddish brown or purplish above, strigillose, the hairs 0.1–0.2 mm long, throughout in the inflorescence, glabrate below, then strigillose in raised descending lines from the decurrent petiole bases, with an admixture of erect to slightly appressed glandular hairs, 0.1–0.2 mm long, mostly in the inflorescence, occasionally throughout, rarely glabrous. Leaves opposite, alternate above, thin, green, lanceolate to narrowly ovate (0.6–)1.3–6.5(–7.5) cm long, (0.3–)0.6–2.6(–3.1) cm wide, acuminate to acute at the apex, remotely, irregularly serrulate with (8–)10–22 teeth on each side, obtuse to rounded, subcordate or occasionally cordate at the base, glabrous or with a few scattered strigillose hairs on the margins, the lateral veins 4–5(–7) on each side of the midrib, on petioles 0–3 mm long. Inflorescence erect, often branched, rarely somewhat nodding, the leaves subtending the flowers much reduced, acuminate, and usually narrower. Flowers erect. Ovaries often reddish purple, strigillose, usually with an admixture of erect to appressed glandular hairs, (0.8–)1–2.2 cm long, on pedicels 2–5 mm long. Floral tube often reddish, 0.9–1.5 mm deep, (0.8–)1.2–2.2 mm across, externally strigillose, usually with an admixture of erect to appressed glandular hairs, internally usually with a ring of erect villous hairs, 0.1–0.2 mm long near the base, often with only a few hairs present and occasionally glabrous. Sepals often reddish, lanceolate, 1.8–2.8 mm long, 0.8–1.2 mm wide, strigillose, usually with an admixture of erect to appressed glandular hairs. Petals white, often flushed with pink after anthesis, or pink, obovate, 3.0–4.5 mm long, 1.5–2.5 mm wide, the notch 0.7–1.5 mm deep. Anthers cream to white, 0.5–0.7 mm long, 0.4–0.5 mm wide; filaments cream to white, those of the longer stamens 1.5–2.2 mm long, those of the shorter 0.8–1.5 mm

long; the longer, and usually the shorter, stamens shedding pollen directly on the stigma before or at anthesis. Style cream to white, 1–1.8(–2.3) mm long; stigma clavate to subcapitate (0.8–)1.5–2.5 mm long, 0.4–0.8 mm thick. Capsules erect, with scattered strigillose and glandular hairs, 3–6.2 cm long, 1–1.6 mm thick, on pedicels 0.4–1.5(–2.2) cm long. Seeds gray brown, narrowly obovoid, 0.9–1.4 mm long, 0.3–0.5 mm thick, with conspicuous longitudinal rows of flattened, fused papillae, at least along the sides, the micropylar end acuminate, the chalazal end with a short appendage, 0.04–0.08 mm long, 0.08–0.2 mm wide; coma white to slightly yellowish, 5–8 mm long, readily detaching. Gametic chromosome number, $n = 18$.

Distribution (Fig. 6): Common and weedy in open, often disturbed areas, usually permanently moist, or at least moist for part of the growing season, such as roadsides, sandy and gravelly stream beds, embankments, boggy areas, and banks of lakes and ponds. In South America, throughout the Andes of Chile and Argentina from central IV Región (Coquimbo), Chile, and San Juan Prov., Argentina, southward to Tierra del Fuego, in the coast range between Santiago and Valparaiso, generally throughout the central valley and coastal hills south of Concepción, scattered eastward on the Patagonian plain in southern Chubut and Santa Cruz Prov., Argentina, and in the Sierra de San Luis and Sierra Grande de Córdoba; also in the Falkland Islands. In North America from Alaska to British Columbia, eastward throughout much of Canada to Labrador, southward through New England to Pennsylvania and parts of the Appalachians, southwestward from Michigan and Indiana across the northern high plains to Colorado and New Mexico, throughout the mountains and basins of the western U.S. to the Pacific coast, south in Mexico along the Sonoran and Chihuahuan deserts to the mountains of southern Mexico and central Guatemala. Also in Japan, Korea, northeastern China, and eastern Siberia. Introduced in Hawaii, Europe and European U.S.S.R., New Zealand, and parts of Australia and Tasmania (Raven & Raven, 1976). In the northern part of its South American range found from 1,200–2,900 m, gradually descending to sea level on the western side of the Andes near Concepción. In the southern part of the range mostly between 200 and 1,900 m, and in Tierra del Fuego from sea level to 350 m. Flowering primarily from December to March throughout, but as early as September in the northernmost parts of the coastal mountains of Chile.

Representative specimens examined: ARGENTINA, CHUBUT: Colonia Sarmiento, *Birabén 555* (LP); Dpto. Cushamén, 30–40 km NE of Esquel, 42°49′S, 71°05′W, *Boelcke et al. 16036* (BAA, MO); Dpto. Futuleufú, Esquel, La Hoya, *Cabrera et al. 25987* (LP); Lago Fontana, *Castellanos in 1932* (BA, MO, RSA); Lago Futalaufquén, *Castellanos in 1945* (F, LIL); Cholila, *Crovetto 3009* (SI); Golondrinas, 42°01′S, 71°31′W, *Crovetto 3197* (BAB, LIL); Valle de Las Plumas, Lago General Paz, *Gerling 43* (BAF); 72 km S of Tecka, crossing Río Cherque, 800 m, *Hjerting 629* (C); Valle del Lago Blanco, 45°54′S, 71°15′W, *Koslowsky 172* (BA); Trevelin, Estancia Río Frío, *Krapovickas 4000* (BAB); Lago Puelo, desembocadura del Epuyén, *Pérez-Moreau in 1940* (BA, LIL, RSA); Parque Nacional Los Alerces, Lago Cisnes, *Pérez-Moreau in 1944* (BA); Lago Epuyén, *Soriano 1374* (BAA, SI); Río Senguer, Estancia Laurita, 44°43′S, 70°04–24′W, *Soriano 1480* (BAA, SI); Dpto. Tehuelches, Arroyo Temenhuao, 44°13′S, 71°16′W, *Soriano 2651* (BAB). CÓRDOBA: *Dpto. San Alberto,* Pampa de Achala, 2,000 m, *Cabrera et al. 16620* (LP); Sierra Grande, cerca del Río Yuspe detrás del Cerro Blanco, 1,650 m, *Hunziker 10253* (CORD, MO, RSA mixed with *E. hirtigerum*); Sierra Achala, Cerro de Los Gigantes, *Kurtz 3879* (CORD, RSA); Sierra Grande, Cuesta de Copina, 1,610 m, 31°50′S, 64°10′W, *Solomon 4149* (MO); Sierra Grande, La Cumbrecita, 1,450 m, 31°55′S, 64°15′W, *Solomon 4199* (MO). MENDOZA: *Dpto. Las Heras,* puente del Inca, Laguna de Los Horcones, *Boelcke et al. 9823* (BAA,

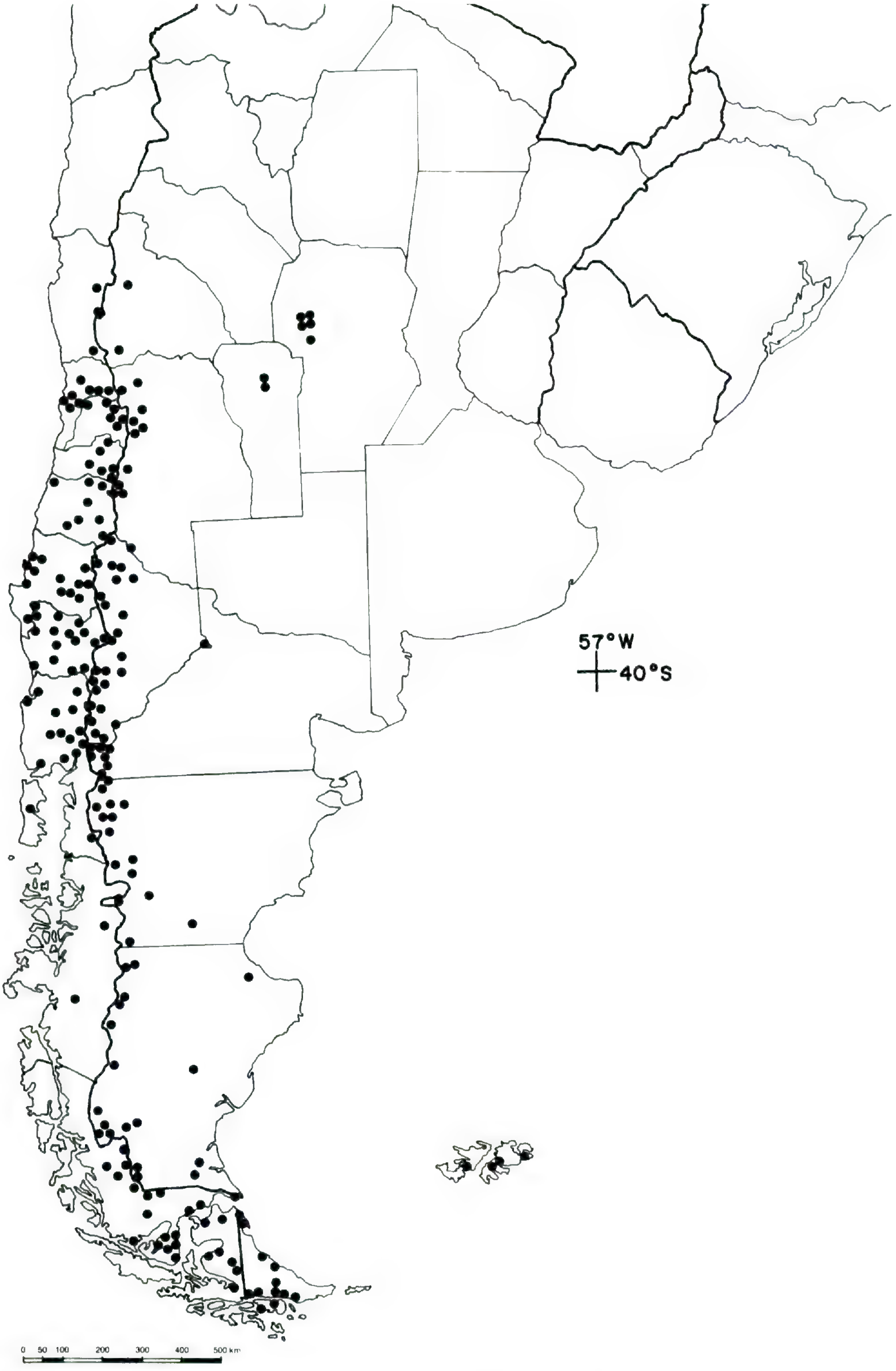


FIGURE 6. Distribution of *Epilobium ciliatum* ssp. *ciliatum* in South America.

BAB, MO). *Dpto. Malargüe*, Arroyo Las Mangas, 2,000 m, *Carette 284* (LP, SI); Dpto. Malargüe, Arroyo del Cordón del Cura, *Castellanos in 1941* (BA, RSA); Dpto. San Carlos, Refugio Gral. Alvarado, 2,000 m, *Cuezzo & Barkley 20MZ451* (NY); Arroyo Chacayco, above Laguna Carilauquén, 36°32′S, 70°11′W, *Kurtz 6086* (JE); Río Salado Superior, Los Molles, *Kurtz 7550* (JE); Dpto. San Rafael, Río Atuel, entre Puesto de Ubilla y Paso del Pico Plateado, *Kurtz 7592* (CORD, JE, LP); Dpto. San Carlos, Arroyo de Yaucha, 33°46′S, 69°02′W, *Kurtz 11153* (CORD); Dpto. Tupungato, Finca Los Helechos, 33°20′S, 69°11′W, *Leal 1259* (LIL); Dpto. Tunuyan, Rincón Colorado, 2,800 m, *Leal 1289* (RSA); Dpto. Tupungato, Estancia La Carrera, 2,350 m, *Melis & Paci in 1949* (BR, G, W); Dpto. Las Heras, Uspallata, 2,000 m, *Semper 540* (LIL, NY); Valle del Atuel, Cajón del Burro, 2,400 m, *Wilczek 412* (G). NEUQUÉN: Lago Nahuel Huapi, Isla Victoria, 770 m, *Boelcke 1795* (BAA, SI); Dpto. Minas Las Ovejas, 37°01′S, 70°45′W, *Boelcke et al. 10752* (BAA, BAB, MO); Dpto. Minas, Laguna Epulauquén, 1,300 m, 36°50′S, 71°04′W, *Boelcke 10856a* (BAA, BAB, MO); Dpto. Chos Malal, Vegas del Pelán, 1,700 m, 36°54′S, 70°20′W, *Boelcke et al. 11140* (BAA, BAB, MO); Dpto. Minas, Varvarco Campos, Arroyo Benítez, 36°17′S, 70°39′W, *Boelcke et al. 14224½* (BAA, MO); confluencia de los Ríos Neuquén y Varvarco, Invernada Vieja, *Boelcke et al. 14439* (BAA, BAB); Arroyo Chacayco, 37°05′S, 69°45′W, *Chicchi 91* (LP); Río Limay, *Chicchi 193* (LP); Dpto. Huiliches, Volcán Lanín, Arroyo Rucu-leufú, *Correa et al. 5596* (BAB mixed with *E. australe*); Parque Nacional Lanín, Baños de Epulafquén, *Correa et al. 5843* (BAB); Pampa del Malleo, 39°48′S, 70°58′W, *Crovetto AN-128* (CTES); Rahue, Estancia Ochoa, 39°23′S, 70°49′W, *Dawson & Schwabe 2129* (BAA, BAB); Hua-Hum, *Dawson & Schwabe 2352* (BAA, BAB; mixed with *E. puberulum*); 10 km from Junín de Los Andes towards Zapala, 900 m, *Hjerting 6306* (C); Neuquén, *Jergensen 636* (BAB); Lago Lolog, *Kalela 1756* (H); Dpto. Ñorquín, Cajón de Trolope, 37°46′S, 71°04′W, *Kurtz 6184* (CORD, JE); Parque Nacional Lanín, San Martín de Los Andes, Cerro Chapelco, 1,700 m, *León & Calderon 978* (BAA); Cerro de Copahue, Fuente Zulena, *O'Donell 2072* (LIL); Dpto. Los Lagos, Villa La Angostura, *Pedersen 1547* (BR, C, MO, P, US); Lago Nahuel Huapi, Peninsula Quetrihue, *Pérez-Moreau in 1940* (BA, RSA); Dpto. Catán-Lil, Estancia Bernal, Arroyo del Cañadón, 39°34′S, 70°36′W, *Pérez-Moreau 3077* (BAB); Dpto. Chos-Malal, Canchahuinganco, 37°01′S, 70°23′W, *Ragonese 166* (BA, RSA); Dpto. Loncopué, Cajón Chenque Pehuén, 38°06′S, 70°55′W, *Rugolo & Agrasar 130* (BAA); Dpto. Catán-Lil, Cerro Chachil, 39°05′S, 70°38′W, *Rugolo & Agrasar 372* (BAA, MO); Lago Nahuel Huapi, Brazo Huemul, Arroyo Huelta, 40°58′S, 71°22′W, *Solomon 4623* (MO); Camino El Huecú a Loncopué, 1,000 m, *Spegazzini 175* (BAB); Dpto. Picunches, Pino Hachado, Arroyo Haichol, *Valla et al. 3009* (BAA, CTES, MO); Lago Quillén, *Valla et al. 3204* (BAA, CTES, MO). RÍO NEGRO: Parque Nacional Nahuel Huapi, Laguna Frías, 41°05′S, 71°50′W, *Boelcke & Correa 5379* (BAA, BAB, SI); Bariloche, 770 m, *Buchtien in 1905* (BAF, BP, BREM, E, F, GB, GH, JE, L, M, PR, S, SI, US, W, Z), *Cabrera 5942* (F, GH, LP, NY, POM, US); Parque Nacional Nahuel Huapi, Lago Fonck, *Pérez-Moreau in 1942* (BA, RSA); Cascada del Mallín Ahogado, El Bolsón, *Scolnik 318* (LIL); Cerro V. Lopéz, W of Bariloche, 1,000 m, 41°03′S, 71°35′W, *Solomon 4611* (MO); Villa Cerro Catedral, 1,030 m, 41°10′S, 71°28′W, *Solomon 4613* (MO); Río Llogdconto, 41°22′S, 71°30′W, *Solomon 4630* (MO); Cerro Tronador, 1,200 m, *Solomon 4637* (MO); 3.9 km S of Campamento La Veranada, 1,000 m, 41°28′S, 71°28′W, *Solomon 4642* (MO); Dpto. Pilcaniyeu, Pilcaniyeu, Estancia Raylluso, *Vallerini 424* (BAA). SAN JUAN: Dpto. Iglesia, El Rodeo, 30°12′S, 69°06′W, *Cuezzo 1848* (LIL); Dpto. Calingasta, Cordillera del Espinazito, Los Manantiales, 2,770 m, 32°14′S, 69°58′W, *Kurtz 9610* (BAF, CORD); Dpto. Calingasta, Las Lumbreras, 2,000 m, *Spegazzini 655* (BAB). SAN LUIS: Sierra de San Luis, Cerro Canutal, 32°46′S, 66°05′W, *Castellanos in 1929* (BA); Cerro Sololosta, 32°51′S, 66°00′W, *Pastore 84* (SI). SANTA CRUZ: Chonque-Aike, 49°16′S, 69°45′W, *Ameghino in 1898* (LP); Dpto. Lago Argentino, Estancia María Elisa, 50°20′S, 71°60′W, *Ancibor & Vizinis 4626a* (BAA, MO); Dpto. Río Chico, Lago Pueyrredón, Río Oro, 500 m, *Boelcke et al. 12897* (BAA, BAB); Dpto. Lago Buenos Aires, 29 km NW of Perito Moreno, 46°25′S, 71°09′W, *Boelcke et al. 16097* (BAB, MO); Camino a Paso Roballos, 47°11′S, 71°36′W, *Boelcke et al. 16176* (BAA, MO); Dpto. Lago Argentino, Lago San Martín, Estancia Cancha Rayada, 48°54′S, 72°26′W, *Boelcke et al. 16293* (BAB, MO); Tehuelches, 250 m, 46°50′S, 67°27′W, *Donat 283* (BM, CAS, F, G, GB, GH, K, MO, NY, S, SI, U, UC, Z); Cerro Buitreras, 51°43′S, 70°09′W, *Hauthal in 1899* (CORD); Between Cerro del Fraile and Cordón de Los Cristales, 50°32′S, 72°39′W, *James 471* (BM, DS, SI); Cerro Buenos Aires, 350 m, 50°24′S, 72°59′W, *James 3004* (BM); Río Coyle, Hotel Las Horquetas, 51°24′S, 70°17′W, *Rahn 4396* (C); Río Los Antiguos, 300 m, 46°32′S, 71°38′W, *Roivainen 2526* (H). El Calafate, 190 m, 50°20′S, 72°15′W, *Solomon 4653* (MO); Glaciar Perito Moreno, 190 m, 50°28′S, 73°02′W, *Solomon 4658* (MO); Lago Volcán, Estancia El Rincón, 47°46′S, 72°15′W, *Spegazzini 324* (BAB); Dpto. Güer Aike, Estancia Stag River, 51°34′S, 71°57′W, *T.B.P.A. (Boelcke et al.) 3280* (BAB, MO, RNG); Pto. Tres Marías, 700 m, 51°28′S, 72°05′W, *T.B.P.A. (Ambrosetti & Mendez) 3680* (MO); Lago Argentino, Brazo Onelli, 300 m, *Vervoorst 4560* (LIL, S, W). TIERRA DEL FUEGO: Río Grande, *Expedición Fac. de Ciencias E.F.y N. 140* (BA); Estancia Harberton, 30 m, *Goodall 71* (LP, RNG); Río Lashifashaj, Brown's sawmill on Ruta O, 40 m, *Goodall 585* (E, LP, MICH, NA, RNG, RSA, UC, US); Estancia Moat, *Goodall 641* (MICH, NA, RNG, SI, UC, US, WIS; mixed with *E. australe*); Estancia Viamonte, Estero Manantiales,

Goodall 906 (NA, RNG); Estancia Cullen, Río Cullen, *Goodall 3180* (LTR, NA); Estancia Cullen, Arroyo Beta, *Goodall 3224* (MICH, NA, RNG, UC); Lago Fagnano, *Hunziker 6711* (BAB, UC). Bahía Lapataia, *Pérez-Moreau in 1948* (BA, MO, RSA); 1 km NW of Ushuaia, 50 m, *Solomon 4712* (MO); Ushuaia, Arroyo Buena Esperanza, 150 m, *Solomon 4741* (MO).

CHILE, IV REGIÓN (COQUIMBO): *Choapa*, Cuncumén, 1,050 m, 31°55′S, 70°35′W, *Solomon 4273* (MO). *Limarí*, Cordillera de Hurtado, 30°30′S, 70°30′W, *Gay 523* (P); Río Gordito, 3,000 m, 31°02′S, 70°20′W, *Jiles 2548* (CONC). V REGIÓN (ACONCAGUA): Los Andes, 10 km W of Río Blanco, 32°55′S, 70°19′W, *Hutchison 131* (UC, US); Los Andes, *Philippi in 1882* (SGO). *Petorca*, Cerro Chache, 18 km E of La Ligua, 1,900 m, *Morrison 17050* (G, GH, K, MICH, MO, NA, UC, WTU). *Quillota*, Limache, Cajón Grande, *Boelcke 432* (BAA, SI). *San Felipe*, San Felipe, *Claude-Joseph 2488* (US). *Valparaíso*, Camino a Laguna Verde, 33°06′S, 71°41′W, *Behn in 1930* (CONC); Concón, *Garaventa 500* (BH, CONC); Cerro del Colliguay, 33°12′S, 71°07′W, *Jaffuel 656* (GH); Valle de Marga-Marga, *Jaffuel & Pirión 3094* (GH). REGIÓN METROPOLITANA (SANTIAGO): *Cordillera*, Río Yeso, Laguna Los Piuquenes, 2,500 m, *Biese 808* (LIL, NY); El Volcán, 1,300 m, 33°50′S, 70°12′W, *Burkart 9346* (SI); San José de Maipo, 1,050 m, 33°40′S, 70°20′W, *Solomon 4313* (MO). *Melipilla*, Las Vizcachas, 10 km from La Dormida, 1,860 m, *Morrison 16779* (G, GH, MO, NA, S, SI, UC). *Santiago*, 5 km above Farellones, La Parva, 2,700 m, *Moore 397* (LA, MO); Maitenes, Pérez Caldera, 1,800 m, 33°11′S, 70°29′W, *Skottsberg & Sparre 11082* (CONC, S); Junction of road to La Disputada with road to Farellones, 1,400 m, 33°20′S, 70°20′W, *Solomon 4291* (MO). VI REGIÓN (O'HIGGINS): *Cachapoal*, Río Coya above El Teniente, 2,900 m, *Pennell 12307* (GH, PH, SGO); Baños de Cauquenes, *Pérez-Moreau in 1948* (BA, MO, RSA). *Colchagua*, San Fernando, *Bertero 237* (P); Termas Vegas Del Flaco, 1,750 m, *Mahu 9747* (H, MO, UC); Rincón de Tinguiririca, *Ricardi in 1950* (CONC, LIL); 19.3 km above La Rufina, 1,000 m, 34°55′S, 70°30′W, *Solomon 4330* (MO). VII REGIÓN (MAULE): *Curicó*, La Montaña, 34°54′S, 70°54′W, *Mahu 10756* (MO); Cordillera del Planchón, *Née in 1793* (MA, mixed with *E. glaucum*); 6.2 km above Los Queñes, 780 m, 35°00′S, 70°45′W, *Solomon 4332* (MO). *Linares*, Panimávida, 35°45′S, 71°25′W, *Philippi in 1883* (BM). Quinamávida, prope Parral, *Philippi in 1893* (JE, SGO); Cajón Troncoso, 36°20′S, 70°45′W, *Schlegel 3695* (CONC). *Talca*, Cordillera de Talca, El Picazo, *Barros 84* (GH); 52.4 km above El Colorado, 900 m, 35°50′S, 70°55′W, *Solomon 4338* (MO). VIII REGIÓN (BÍO-BÍO): *Arauco*, Laraquete, 37°10′S, 73°11′W, *Hosseus 85* (CORD); Contulmo, Lago Lanalhue, *Ricardi in 1949* (CONC, LP; mixed with *E. puberulum*). *Bío-Bío*, Entre Cabrero y Salto del Laja, 37°07′S, 72°23′W, *Marticorena et al. 852* (CONC, MO); Dpto. La Laja, Cuñibal Oriente, 150 m, 37°31′S, 72°15′W, *Marticorena et al. 874* (CONC, MO); Camino de Santa Barbara a Río Huequecura, Puente Piulo, 290 m, 37°42′S, 72°00′W, *Marticorena et al. 891* (CONC); Estero Epún, 1,260 m, 37°52′S, 71°28′W, *Marticorena et al. 970* (CONC, MO); On road to Laguna La Laja, 1,400 m, 37°25′S, 71°20′W, *Solomon 4434* (MO); Antuco, 530 m, 37°20′S, 71°40′W, *Solomon 4445* (MO). *Concepción*, Tomé, *Junge in 1935* (CONC); Concepción, *Junge 3016* (US); 5 km SW of Concepción, 200 m, *Skog 1030* (CONN); 9.7 km W of San Rafael, 450 m, 36°35′S, 72°45′W, *Solomon 4403* (MO). *Ñuble*, Termas de Chillán, Garganta del Diablo, *Gleisner 162* (CONC, MO); Termas de Chillán, 1,720 m, *Moore 412* (LA, MO), 2,200 m, *Werdermann 1314* (E, K, NY, S, UC, US, Z; mixed with *E. australe*); 8.2 km E of San Rafael, 300 m, 36°35′S, 72°45′W, *Solomon 4395* (MO). IX REGIÓN (ARAUCANÍA): *Cautín*, Desembocadero del Río Toltén, 39°15′S, 73°14′W, *Friedrich in 1934* (CONC); 4 km SW of Termas de Palguín, 780 m, *Moore 302* (LA, MO); Temuco, banks of Río Cautín, *Roivainen 2994* (H); Puente Correntoso, 15 km E of Villarrica, 210 m, 39°16′S, 72°00′W, *Solomon 4536* (MO); Pitrufquén, 100 m, 38°59′S, 72°39′W, *Sparre 3454* (S). *Malleco*, Cordillera de Nahuelbuta, Los Alpes, Fundo Solano, 590 m, *Eyerdam 10296* (NY); Parque Nacional de Nahuelbuta, Pino de Canales, *Mahu 5860* (MO); Arroyo Lumaco, Capitán Pastene, 100 m, 38°11′S, 73°00′W, *Marticorena et al. 1224* (CONC); Entre Pino Hachado y Liucura, 1,080 m, *Marticorena et al. 1434* (CONC); Dpto. Victoria, Termas de Tolguaca, 1,180 m, *Morrison & Wagenknecht 17500* (G, GH, MO, S, SI, UC); Curacautín, 700 m, *Pennell 12715* (F, GH, NY, PH, SGO); Buenavista below Volcán Tolguaca, 1,100 m, *Pennell 12815* (F, GH, NY, PH, SGO); Pidima, Fundo Chequenco, *Pfister in 1946* (CONC); Laguna San Pedro, Lonquimay, *Pinto in 1953* (CONC); 2.8 km below Vegas Blancas, 37°45′S, 72°58′W, *Solomon 4472* (MO); 30 km W of Curacautín, 500 m, 38°20′S, 72°05′W, *Solomon 4472* (MO); 30 km W of Curacautín, 500 m, 38°20′S, 72°05′W, *Solomon 4473* (MO); Termas del Río Blanco, 1,300 m, 38°35′S, 71°35′W, *Solomon 4496* (MO); Lago Icalma, 1,000 m, 38°48′S, 71°16′W, *Zöllner 7868* (MO). X REGIÓN (LOS LAGOS): *Chiloé*, Castro, *Gay 63* (P); Piruquina, *Junge 291* (CONC). *Llanquihue*, Paso Pérez Rosales, 980 m, *Moore 325* (LA); Camino Ensenada a Ralún, *Pfister in 1946* (CONC); Calbuco, *Philippi in 1893* (JE, SGO); Río Maullín, *Wall in 1947* (GB). *Osorno*, Salto Pilmaiquén, *Rudolph in 1931* (VALD); Chuyaca, 40°34′S, 73°07′W, *Rudolph in 1933* (VALD); Ñadi Caipulli, *Rudolph in 1951* (VALD); 7.7 km E of Puyehue, 200 m, 40°40′S, 72°18′W, *Solomon 4592* (MO); Lago Constancia, 1,000 m, *Sparre & Smith 353* (CONC, mixed with *E. australe*). *Palena*, Río Palena, *Delfin in 1887* (SGO). *Valdivia*, Cordillera de Ranco, *without collector (844) in 1852* (GOET, JE); Corral, 30 m, *Gunckel 3195* (BH); Lago Puyehue, Isla Fresia, *Mahu in 1956* (MO); Camino de Coñaripe a Puerto Fui, Km 6, *Marticorena et al. 473* (CONC); San Juan, 40°15′S, 73°05′W, *Philippi in 1887* (SGO);

Valdivia, *Philippi in 1888* (CORD, K, US). XI REGIÓN (AISÉN): *General Carrera,* Valle León, Lago Buenos Aires, 550 m, *von Rentzell 6242* (GH, SGO, SI); Ventisquero Soler, 500 m, 46°52′S, 73°08′W, *Seki 547* (CONC). *Coihaique,* Lago Seco, 45°35′S, 72°02′W, *Schlegel 2345* (CONC). XII REGIÓN (MAGALLANES): *Antártica Chilena,* Isla Navarino, 3 km W of Puerto Williams, 100 m, *Moore 353* (LA, MO); Isla Navarino, Puerto Douglas, 55°10′S, 68°08′W, *Vervoorst 385* (LIL). *Magallanes,* Morro Chico, 52°02′S, 71°26′W, *without collector or date* (WU); Seno Otway, Río El Canelo, *Biese 1249* (LIL); Río Tres Brazos, 10 m, 53°16′S, 71°02′W, *Cekalovic 90* (CONC); Bahía Santiago, *Cunningham in 1867* (S); Neighborhood of Monte Dinero, 52°19′S, 68°36′W, *Cunningham in 1868* (NY); 80 km NE of Punta Arenas, 25 m, *Eyerdam et al. 23935* (G, GH, NA, UC); Mina Loreto, near Punta Arenas, 150 m, *Mexia 7979* (BM, GB, GH, K, MO, NY, S, UC); Isla Riesco, Estancia Río de Los Palos, 53°26′S, 73°30′W, *Pfister & Ricardi in 1952* (CONC); Fiordo Silva Palma, Angostura Titus, Río Raul, *Pisano 3752* (HIP, MO, RNG); Seno Skyring, Estancia Skyring, *Pisano 4383* (HIP, MO); 8 km W of Aguas Frescas, 100 m, 53°20′S, 71°05′W, *Solomon 4685* (MO); Laguna Parrillar, 350 m, 53°20′S, 71°08′W, *Solomon 4686* (MO); 2 km W of Puerto Hambre, 20 m, 53°40′S, 70°55′W, *Solomon 4689* (MO). *Tierra del Fuego,* Bahía San Felipe, *Cunningham in 1867* (K); Estancia Vicuña, Cerro Bahamondes, 300 m, *Goodall 1756* (MICH, NA, RNG, UC, US); South of Cerro Sombrero, 52°46′S, 69°18′W, *Goodall 2060* (LTR, NA); Bahía Inútil, Estancia Camerón, 53°38′S, 69°39′W, *Moore 1076* (CAS, GH, RNG); Lago Blanco at Río Blanco, *Moore 1098* (CAS, RNG); Aserradero Río Bueno, 53°40′S, 69°55′W, *Pisano 2486* (CONC, HIP, RNG); Río Fontaine, 54°29′S, 68°59′W, *Skottsberg 122* (UPS). *Última Esperanza,* Estancia Cerro Castillo, Lago Porteño, *Moore 1023* (DS, RNG, S, SGO); Estancia Bories, Lago Escondido, 51°55′S, 72°09′W, *Moore 1028* (DS, RNG, US); Río Rubens, *Kalela 2088* (H); 2 km E of Puerto Cóndor, 51°38′S, 72°40′W, *Solomon 4703* (MO); Estancia Cerro Castillo, Lago Sofia, 51°32′S, 72°37′W, *T.B.P.A. (Latour et al.) 1508* (BAB, MO); Seno Última Esperanza, Puerto Toro, 51°25′S, 73°04′W, *T.B.P.A. (Moore & Pisano) 1896* (BAB, MO, RNG).

FALKLAND ISLANDS, Without locality, *Hooker in 1842* (BM, E, G, K, P). EAST FALKLAND: Goose Green, ca. 3 mi SE of Bodie Creek House, *Moore 612* (RNG); Darwin, *Moore 640* (DS, GH, LP, S, UC). Port Harriet, *Wright* (K). WEST FALKLAND: Fox Bay, *Vallentin in 1910* (K).

In southern South America, *Epilobium ciliatum* subsp. *ciliatum* is an extremely widespread, weedy, highly polymorphic taxon. Despite its variable nature, this species possesses many features that clearly distinguish it from other taxa. Most plants produce turions or leafy rosettes below or at the ground surface as overwintering structures, a feature that is not present in any other native South American species. This, combined with the presence of seeds with longitudinal lines of fused, flattened papillae, erect glandular-pubescent inflorescences, and small white to pink flowers, serves to separate *E. ciliatum* from other species with which it might be confused. Two species in particular, *E. obscurum* and *E. australe,* are often mistaken for *E. ciliatum,* especially when the specimens lack underground parts. *Epilobium obscurum* produces leafy basal shoots and has a densely strigillose inflorescence with glandular hairs restricted to the floral tube, rose purple petals, and narrowly lanceolate, denticulate leaves. Some plants of *E. ciliatum* from higher elevations or exposed sites are especially easy to confuse with *E. australe,* because their leaves are relatively small with few teeth, more congested, thicker, and the plants often are low in stature (less than 20 cm). *Epilobium australe* is shortly rhizomatous with leafy basal shoots; it completely lacks glandular pubescence and has thick, few-toothed, ovate leaves. *Epilobium obscurum* and *E. australe* have seeds without lines of fused papillae.

Many names have been given to the forms of *E. ciliatum* in South America. Most of these were proposed at a time when the number of collections was small, and each of the taxa appeared more or less homogeneous. For example, *E. chilense* was based on large-leaved, robust, densely glandular plants from central Chile, while *E. valdiviense* was drawn from specimens from the same area that were more graceful, less pubescent, with the leaves shorter than the internodes. In his monograph, Haussknecht (1884) recognized only three taxa in this complex

in South America. Subsequently, other names were proposed piecemeal for more or less distinctive populations or because of a lack of literature or understanding of previously published names.

Samuelsson (1923) recognized all of Haussknecht's taxa plus two others and, in addition, proposed five new species. These new taxa were either from remote areas or had distinctive morphological features that separated them from the other taxa with which Samuelsson was familiar. He placed a great deal of emphasis on the density of pubescence, leaf size and disposition, and branching patterns in separating his taxa; these features are extremely plastic within this subspecies.

The relationship of South American collections to North American taxa has been uncertain historically. Haussknecht, in his original description of *E. adenocaulon,* listed a collection from Aconcagua Prov., Chile (*R. Philippi,* W) among the four collections cited, with the other three from North America (Haussknecht, 1879). Later, in his monograph (Haussknecht, 1884), he re-identified this specimen as *E. chilense* but then cited a collection from Missoula, Montana (*Krause,* JE) under the latter name. Samuelsson (1923) later reassigned the Montana plants to *E. adenocaulon.* Apparently after publication of his monograph, Haussknecht annotated a few additional collections from Chile as *E. glandulosum* (Reiche, 1898) and *E. adenocaulon* (e.g., Castro, Chiloé Prov., Chile, *Gay 63,* P).

The relationship of the South American populations to those in North America was brought up again when it was learned that the seeds of *Epilobium chilense* shared a peculiar feature, the presence of longitudinal ridges of flattened, fused papillae, with the *E. ciliatum* complex (*E. ciliatum,* including *E. glandulosum* and *E. watsonii*; and *E. oreganum*; Seavey et al., 1977). This, combined with fleshy-leaved turions in both South and North American plants, strongly suggested that *E. chilense* was very closely related to *E. ciliatum,* if not conspecific (Seavey & Raven, 1977c).

Hoch (1978) examined the *Epilobium ciliatum* complex in North America, especially *E. ciliatum* itself. Plants of this species had long gone under a plethora of names, in particular *E. adenocaulon* and *E. glandulosum.* Hoch's study made it clear that the many taxa recognized from North America could not be recognized and still maintain a functional, information-rich taxonomy. As a result, *E. ciliatum* was reduced to a series of three modally and geographically distinct but intergrading subspecies.

In light of the careful work of Hoch and an examination and comparison of the bulk of the available South American material with a broad spectrum of North American populations, it is clear that the many taxa proposed from South America can be reduced to the single variable taxon *E. ciliatum* subsp. *ciliatum* as circumscribed by Hoch (1978). Indeed, some plants are almost indistinguishable (e.g., Yellowknife, Mackenzie Territory, Canada, *Cody & McCanse 3327,* MO, and near Paso Puyehue, Osorno Prov., Chile, *Solomon 4593,* MO; Kyle Canyon, Charleston Mtns., Clark Co., Nevada, *Goodman & Hitchcock 1707,* MO, and Vegas Blancas, west of Angol, Malleco Prov., Chile, *Solomon 4450,* MO; Rattlesnake valley, Missoula Co., Montana, *Barkley 1887,* MO, and Cerro Tronador, Río Negro Prov., Argentina, *Solomon 4640,* MO; Drummond Is., Chippewa Co., Michigan, *McVaugh 9143,* MO, and Río Blanco, north end of Lago Blanco, Tierra

del Fuego Prov., Chile, *Moore 1098,* RNG; Hawks Ranch, 25 mi S of Laramie, Albany Co., Wyoming, *Churchill in 1918,* MO, and between Cerro Blanco and La Hollada, Córdoba Prov., Argentina, *Solomon 4096,* MO; Ruby River, 30 mi S of Varney, Madison Co., Montana, *Parker 7033,* MO, and 8 km W of Aguas Frescas, Magallanes Prov., Chile, *Solomon 4685,* MO). These examples cover the full range of overlapping morphological characters found in North and South American plants, from simple to branched, densely glandular-pubescent to sparsely strigillose, and in size from 4 cm to over 40 cm.

Although there is considerable overlap in morphological features, two components, leaves and turions, are modally slightly different from populations in North America. The majority of South American plants produce fleshy-leaved turions just below the ground surface. This is especially prevalent at higher elevations and latitudes. Plants with leafy rosettes at the ground surface are found throughout the range. However, they form only a small portion of the plants from the southern part of the distribution of *Epilobium ciliatum* and are only frequent in the northernmost populations and in the coastal mountains and at low elevations (i.e., below about 1,000 m). Similarly, the leaves of plants from higher elevations and latitudes in South America show a tendency to be slightly thicker, generally shorter and proportionately broader, with fewer marginal teeth than many North American populations. Again, this is only a trend, with plants of very similar morphology appearing in North America, but not as often. The same trend from leafy rosettes toward condensed turions is also seen in North American populations, especially in cold or extreme habitats (Hoch, 1978).

In general, although *E. ciliatum* subsp. *ciliatum* in South America is quite variable, the overall diversity of morphological types represented is not as great as that found in North America and many of the conspicuously distinctive morphological types now included in subsp. *ciliatum* of North America are not present (e.g., *E. holosericeum, E. ecomosum*). It seems most likely that *E. ciliatum* is a fairly recent, possibly late Pleistocene or even Holocene, arrival in South America by means of long-distance dispersal. While it has diversified to some extent, the reduced variability of morphological types encountered probably reflects the relatively limited genotypic diversity of its founding population.

The most extreme range of variability in *E. ciliatum* is found in stature and branching patterns. Not only do these differ from one population to the next, but they are usually conspicuous within populations, depending on the location of an individual: in shade or full sun, at the edge of a stream, in a bog, or on a drying gravel bar. Plants are often simple, especially when small, but generally branch above or from below later in the growing season. Secondary branching can be extremely dense and prolific when the terminal shoot is damaged, giving the plants a bushy appearance. Low plants, ca. 15 cm tall, with this type of branching formed the basis of the name *E. magellanicum*.

Since *E. ciliatum* is perennial, turions or leafy rosettes as overwintering structures are produced late in the season. The dead scales of the previous year's turions usually persist around the base of the stem, often several centimeters under the ground surface, but these are frequently lost when specimens are gathered. Because *E. ciliatum,* like most other *Epilobium* species, will germinate, grow, and reproduce in a single season, many plants collected early in the growing

season or on newly formed, disturbed sites may appear to be annual, without any indication of perennating structures. It is certainly possible that individuals in particularly marginal habitats may be facultatively annual and do not produce overwintering structures at all.

Within a given population there is frequently an enormous disparity in size of the individuals. For example, an extensive population at the Termas de Chillán, Ñuble Prov., Chile (*Solomon 4373, 4376*) produced plants from less than 6 cm to more than 60 cm tall, all actively flowering and producing fully mature capsules. There were many more small and medium-sized individuals than large ones. This pattern is frequent throughout the range of *E. ciliatum* although not necessarily in every population.

Variation in the size of herbaceous plants has always posed a problem for taxonomists, especially when dealing with limited material that does not cover the full range of morphological diversity. Per Dusén described *Epilobium santa-cruzense* from several dozen plants between 5 and 10 cm tall, collected "in uliginosis" from the upper valley of the Río Santa Cruz. He compared them with *E. anagallidifolium*, but suggested that their seeds were very similar to *E. saximontanum*, a member of the *E. ciliatum* complex. Although these plants are quite distinctive when taken by themselves, they have been retained in *E. ciliatum* because populations from slightly further west around Lago Argentino (*Solomon 4653, 4658*, MO) contain plants of very similar morphology as well as a continuously intergrading series of larger plants. The seeds of *E. santa-cruzense* have the conspicuous ridges typical of *E. ciliatum*.

The extent to which size differences, as seen in *Epilobium ciliatum*, are genetically controlled is not known. In a recent study of an annual, out-crossing species of *Stephanomeria*, Gottlieb (1977) showed that there was no apparent genetic difference between small and large members of a single population, and that size and seed production were regulated by environmental factors.

It is certainly possible that a similar situation occurs in *Epilobium ciliatum*. In a series of collections from Villa Cerro Catedral, Río Negro Prov., Argentina (*Solomon 4613, 4614, 4615*, MO), plants from a level sandy area, which had once been wet, were mostly less than 7 cm tall, with small flowers and densely leafy stems. Only a few meters away, at the edge of a small stream, plants 30 to 40 cm tall, with long internodes and larger flowers were found. In between were plants of intermediate stature, their size apparently depending on the available soil moisture. The high rate of autogamy in *E. ciliatum* undoubtedly must have some impact on the genotypes available for each succeeding generation, but its significance is not known. A study similar to that conducted on *Stephanomeria exigua* Nutt. would be well worth the investigation.

Stem vestiture also shows significant variation. In general, *Epilobium ciliatum* has both glandular and strigillose pubescence, although both types may be sparse, or the glandular hairs may be restricted to just the ovaries. Only rarely are completely glabrous plants encountered, such as those on which Samuelsson based his *E. leiophyton*. The density of the glandular pubescence seems to have some geographical basis. Plants from lower elevations in the central valley and coastal range in the northern portion of the Chilean distribution (mostly north of Valdivia) are often densely glandular-pubescent (e.g., Concón, Valparaíso Prov., Chile,

Garaventa 500; Limache, Quillota Prov., Chile, *Looser 2007, 2011*; Corral, Valdivia Prov., Chile, *Gunckel 15169*; 44 km E of El Colorado, Talca Prov., Chile, *Solomon 4339*; 30 km W of Curacautín, Malleco Prov., Chile, *Solomon 4473*). Within this distribution, densely glandular plants are frequent and often characterize entire populations. At higher elevations and further to the south, glandular hairs are less dense, and the dense type does not appear in Argentina at the same latitude. Although pubescence is not an insignificant feature and does apparently have a geographical basis, it is not useful to recognize these plants in a formal way, because the variation in other characters is indistinguishable from that found in other populations, and pubescence density is often a quantitative and plastic character. The only evident correlation for the presence of densely glandular plants may be due to their occurrence in the warmest and driest portions of the range of *E. ciliatum* in South America, although the functional significance of most hair types in plants is very poorly known (Ehleringer et al., 1976; Levin, 1973).

Epilobium ciliatum typically has small, highly autogamous flowers that show little variation in size. Like the turions and leaves discussed earlier, the color of the petals also varies geographically. Low-elevation plants from the central valley and coast range of central Chile have white flowers that flush only a faint pink, or not at all, after anthesis. Those from higher places in the Andes at this same latitude are also usually white at anthesis, but these may fade to a darker pink afterward. As one moves southward along the Andes, beginning in the vicinity of San Carlos de Bariloche, plants with pink flowers at anthesis become increasingly common, so that populations from Santa Cruz Prov., Argentina, adjacent Chile, and Tierra del Fuego are all pink flowered. Pink flowered populations may also be found further north, but only at higher elevations. The pink petal color is produced by malvidin-3-5-diglucoside (Harborne, 1967), the presence and abundance of which, in the case of *E. ciliatum,* is possibly environmentally controlled. The genes that control pigment production are perhaps induced under the influence of decreasing temperatures, or increased ultraviolet radiation at high elevations or latitudes. Transplants of turions from pink flowered plants (Ushuaia, Tierra del Fuego, Argentina, *Solomon 4712*; grown as M1856 in 1979), under greenhouse conditions, produced white flowers. Seed from two other pink flowered populations (near Ventisquero Perito Moreno, Prov. Santa Cruz, Argentina, *Solomon 4656, 4658*; grown as M1850, M1851, in 1979, respectively) also produced only white flowers under greenhouse cultivation.

It is not surprising that a weedy, autogamous species such as *Epilobium ciliatum* should exhibit a substantial amount of variation, both between populations and within a single population. The often disturbed habitats where *E. ciliatum* occurs, such as stream beds, seep, or embankments, over a broad elevational range, are ephemeral, being newly created or altered from one year to the next, and often in a drastic manner, by such agents as flooding. The ability to successfully colonize these localities requires not only high dispersability, but also great genotypic and phenotypic plasticity to cope with a broad spectrum of environmental parameters. It may be safely said that *E. ciliatum* is a superlative example of such an opportunistic species.

Disjunct populations of *Epilobium ciliatum* are found in the Sierra de San Luis

and the Sierra Grande de Córdoba. These undoubtedly originated by long-distance dispersal of seed from the main range of the Andes via the westerly winds. Some of the most robust and largest leaved individuals seen in any population came from the Sierra Grande, where they were found growing in moist ravines (*Solomon 4074, 4096*). All of the populations examined in the Sierra Grande had white flowers. Disjunct populations also occur in the Falkland Islands and must have been derived in a similar fashion from populations to the west. Apparently, *E. ciliatum* is rare and scattered along streams on these islands (Moore, 1968).

Epilobium ciliatum is by far the most common species encountered in the central and southern Andes of Chile and Argentina, where it grows sympatrically with at least nine other species. It overlaps with *E. hirtigerum* and *E. denticulatum,* in the Sierra Grande, and with the latter also in a narrow band along the east side of the Andes in Mendoza and San Juan provinces, Argentina, and in the Sierra de San Luis.

Despite the highly autogamous or even functionally cleistogamous flowers, occasional hybrids with *Epilobium australe, E. barbeyanum, E. denticulatum, E. glaucum, E. hirtigerum, E. obscurum,* and possibly *E. puberulum* do occur. Only hybrids with *E. australe* and *E. glaucum* are discussed here, because they are the most frequently encountered, in part due to their broadly sympatric range with *E. ciliatum* throughout the southern Andes. Details on the other hybrids are found under each of the other species listed above.

All of the species that hybridize with *Epilobium ciliatum,* except *E. denticulatum* and *E. puberulum,* have the BB chromosome arrangement. Hybrids between the two chromosomal groups are usually easily distinguished because of the intermediate morphology and reduced seed set and pollen stainability. Hybrids between *E. ciliatum* and *E. glaucum* (e.g., Arroyo Huelta, Lago Nahuel Huapi, *Solomon 4626, 4627,* MO; and Cerro López, Río Negro Prov., Argentina, *without collector in 1953,* BAB) generally have narrow, few-toothed leaves, strigillose pubescence, sometimes with glandular hairs, and loose, elongate turions. The average pollen stainability for *Solomon 4626, 4627,* and the Cerro López collection was 21%, 19%, and 22%, respectively.

Hybrids between *Epilobium ciliatum* and *E. australe* are more difficult to distinguish, but the reduced seed set or poor capsule development is an indicator of hybrid origin. In hybrids of this combination (e.g., Ea. Achalay, Santa Cruz Prov., Argentina, *T.B.P.A. 2349,* MO, RNG; Río Coyle, Santa Cruz Prov., Argentina, *Dauber 4,* BAA; and Arroyo Beta, Tierra del Fuego, Argentina, *Castellanos in 1942*) have intermediate leaf morphology, usually a few glandular hairs, larger pink flowers, good seeds with few, imperfectly formed ridges, and loose, somewhat elongate leafy basal shoots. The average pollen stainability for *Dauber 4* (BAA), *T.B.P.A. 2349* (MO, RNG), and *Castellanos in 1942* was 19%, 22%, 28%, and 30%, respectively.

6. **Epilobium nivale** Meyen, Reise um die Erde 1:315. 1834. Walp., Reliq. Meyen, 327. 1843. TYPE: Chile, VII Región (Maule), Cerro Imposible, 3,800 m, January–March 1831, *F. Meyen* (JE, lectotype here designated, photograph MO; B (destroyed, photographs BH, GH, MO, NY), BR, K, P, W, isolectotypes). Gay, Hist. Fis. Chile 2:349. 1846. Walp., Repert. Bot. Syst. 5:666. 1846. Hausskn.,

Monogr. *Epilobium* 251. 1884. Reiche, Fl. Chile 2:244. 1898. H. Lév., Iconogr. *Epilobium, tab. 205*. 1911. Samuelsson, Svensk Bot. Tidskr. 17:290. 1923.

E. alpinum auct. non L.: Hook. & Arn., Hook. Bot. Misc. 3:390. 1833.

E. andinum R. Phil., Anal. Univ. Chile 84:747. 1893. TYPE: Chile, VII Región (Maule), Cordillera de Talca, Cuesta de Las Animas, February 1879, *F. Philippi* (SGO-53014, lectotype here designated, photographs GH, MO; SGO-41463, SGO-53021 (specimen in upper right portion of sheet), probable isolectotypes). Philippi's handwritten annotation of *Epilobium andinum* has been seen on six herbarium sheets at SGO, representing three different species, *E. nivale*, *E. australe*, and *E. ciliatum* subsp. *ciliatum*, all potential types for the name *E. andinum*. That all three species were included in the protologue is evidenced by:

1. "El ejemplar más grande del herbario mide 19 centimetros, . . ." (The largest specimen in the herbarium measures 19 cm, . . .). There is one specimen, SGO-53019, which is about 19 cm tall, a collection of *E. ciliatum* subsp. *ciliatum*.

2. "Los ejemplares de la Cordillera de Talca y de La Cueva (Sierra Velluda) son menos altos y echan muchas ramas en su base" (The specimens from the Cordillera de Talca and La Cueva (Sierra Velluda) are smaller and produce many branches from the base). The specimen from La Cueva, SGO-53020, is an example of *E. australe*.

3. In the Latin diagnosis, R. Philippi begins with, "Epilobium glaberrimum; caule tereti; foliis omnibus oppositis, ..." There are three specimens of *E. nivale*, SGO-53014, SGO-41463, and SGO-53021 in upper right, all of which are glabrous and have consistently opposite leaves. Among native South American *Epilobium*, only *E. nivale* and the distinctive *E. glaucum* are glabrous. Based on the Latin diagnosis, it appears that Philippi had the specimens of *E. nivale* specifically in mind, even though he included specimens of two other species in his discussion.

Low, caespitose perennial herb, (5–)10–20(–30) cm tall, from a fibrous root system. Stems numerous, decumbent, terete, simple, occasionally branched above, usually reddish purple throughout or bicolored reddish purple on the upper surface and green on the lower, glabrous. Leaves mostly opposite, alternate only in the inflorescence, thick, dark green, often reddish purple along the margins, narrowly ovate to lanceolate, 0.5–1.6(–2.5) cm long, 1.5–5(–8) mm wide, acute or occasionally obtuse at the apex, remotely denticulate with 1–4 low teeth on each side, acute to cuneate at the base, glabrous, the lateral veins very inconspicuous, none or 1, rarely 2, on each side of the midrib, on petioles 0.5–1 mm long. Inflorescence erect, simple. Flowers erect. Ovaries reddish purple or occasionally bicolored, reddish purple on one half, green on the other, glabrous, 0.5–1.2 cm long, on pedicels 1–6 mm long. Floral tube often reddish-purple, 0.5–0.8 mm deep, 1.2–2 mm wide, glabrous. Sepals often reddish purple, lanceolate, 1.9–2.8 mm long, 0.8–1.3 mm wide, glabrous. Petals pale pink, 2.8–4.5 mm long, (1–)1.4–2.2 mm wide, the notch 0.5–0.9(–1.2) mm deep. Anthers cream, 0.4–0.6 mm long, 0.4–0.5 mm wide; filaments cream, those of the longer stamens 1–1.6 mm long, those of the shorter 0.4–0.8 mm long, the longer stamens shedding directly on the stigma at anthesis. Style cream to white, 1.2–1.6 mm long; stigma cream to white, subcapitate to clavate, 0.6–1.5 mm long, 0.5–0.8 mm thick. Capsules erect, often reddish purple, occasionally bicolored, reddish purple on one half, greenish or light brown on the other, glabrous, 1.1–4 cm long, on pedicels 0.3–1.2(–1.8) cm long. Seeds pale brown, papillose, obovoid, 1.1–1.4 mm long, 0.3–0.5 mm thick, the chalazal end with an appendage, 0.04–0.1 mm long, 0.08–0.15 mm wide; coma white, 2.5–7 mm long. Gametic chromosome number, $n = 18$.

Distribution (Fig. 5): Along rivulets, boggy places, stream banks, and other permanently wet sites in alpine areas, often extending upward to the snow line, occasionally on stable scree, and sometimes extending to slightly lower elevations, especially in the forest regions, along rocky stream beds. In the central

and southern Andes of Chile and Argentina from Paso Portillo (33°S), southward along the mountains to the vicinity of Epuyén, Chubut Prov., Argentina, disjunct to the Torres del Paine region of Chile and Lago Argentino, at elevations of 2,000–3,500 m in the northern portion of its range, gradually descending to 1,200–2,000 m in Río Negro and Chubut, and in the southernmost populations from 350 to 1,200 m. Flowering December to March.

Representative specimens examined: ARGENTINA, CHUBUT: Epuyén, Cuartel Epuyén, *Lourteig & Buchinger 22* (P). MENDOZA: Valle Atuel, Lago Atuel, 3,100 m, *Böcher et al. 1972* (C, DS); Dpto. Las Heras, Las Cuevas, 3,220 m, *Boelcke 9766* (BAA, BAB, MO); Dpto. Malargüe, Paso Pehuenche, *Boelcke et al. 10358* (BAA, BAB, MO); Arroyo en el alto valle, Calmucó, 36°24′S, 69°50′W, *Burkart et al. 14178* (LIL); Tres Esquinas, 33°50′S, 69°00′W, *Carette 285* (LP, SI); Laguna Diamante, 3,200 m, *Carette 286* (LP, SI), *Serra 39* (LP); Valle del Atuel, Cajón del Burro, *Gerth 108* (L, SI); Valle Hermoso, *Kurtz 5860* (CORD, G, JE, NY), *Sosa 13* (SI); Dpto. Malargüe, entre Arroyo Alverjalito y Arroyo Leñas Amarillas, *Kurtz 7160* (CORD, JE, SI); Dpto. San Rafael, Arroyo El Indigeno, 10 km N of Volcán Overo, *Lagiglia 2218* (LP); Dpto. Tunuyán, Valle del Alto Tunuyán, Paso Hondo, *Leal 2059* (LIL); Dpto. San Rafael, Cerro de Los Molles, *Kurtz 7514* (CORD, JE, LP), *Rossi 297* (LIL); *Sleumer 637* (B, LIL). NEUQUÉN: Parque Nacional Nahuel Huapi, Cerro Colorado, entre Pto. Manzano y Lago Traful, *Boelcke & Correa 6909* (BAA, BAB); Norquinco, 2,200 m, 39°08′S, 71°18′W, *Comber 539* (K); Dpto. Lácar, Cerro Chapelco, 1,800 m, *Cabrera 23009* (LP), *Correa et al. 5886* (BAB, MO); Copahue, 1,000 m, *Kraftsik in 1968* (BAB). Paso Pino Hachado, *Parodi 2215* (BAA); Lago Villarino, 40°26′S, 71°36′W, *Roth in 1896* (LP). RÍO NEGRO: Cerro Tronador, Río Manso Superior, *Gentili in 1975* (MO); Cerro Utne, 41°19′S, 71°21′W, *Hosseus 456* (CORD), *463* (CORD); Parque Nacional Nahuel Huapi, Cerro Catedral, 2,000 m, *Pedersen 1488* (C); Cerro V. López, W of Bariloche, 1,500 m, 41°05′S, 71°35′W, *Solomon 4620* (MO). SANTA CRUZ: Estancia Lago Roca, Cerro Fraile, 50°32′S, 72°39′W, *James 427* (BM, DS); Lago Argentino, Cerro Buenos Aires, 50°24′S, 72°59′W, *James 711* (BM), *Skottsberg 945* (UPS); Dpto. Güer Aike, Estancia Las Viscachas, 1,250 m, 50°46′S, 72°08′W, *T.B.P.A. (Arroyo et al.) 2671* (RNG).

CHILE, V REGIÓN (ACONCAGUA): *Los Andes*, Juncal, 32°52′S, 70°10′W, *Buchtien in 1903* (US); Laguna del Inca, *Kurtz in 1886* (JE, LP, NY); Paso Portillo, 2,800 m, *Milner in 1935* (CONC), *Sparre 1687* (S), *Wall in 1946* (A, S). REGIÓN METROPOLITANA (SANTIAGO): *Cordillera*, Vegas del Tupungato, *Behn in 1930* (CONC), *Melin in 1930* (UC); Cerro de San Pedro Nolasco, 33°48′S, 70°16′W, *Gillies* (BM, E, OXF); Laguna Negra, *Vidal in 1873* (SGO); Ski village La Parva, 2,850 m, 33°20′S, 70°18′W, *Moore 395* (LA, MO), *Solomon 4361* (MO). VI REGIÓN (O'HIGGINS): *Cachapoal*, Sewell, 2,400 m, *Bastin 16* (US); Cauquenes, *Gay 188* (P); Río Coya above El Teniente, 2,700 m, *Pennell 12292* (F, GH, NY, PH, SGO); Ventisquero Los Cipreses, 2,000 m, *Reed in 1872* (POM). *Colchagua*, Cordillera de Colchagua, 2,000 m, *Pirion 107* (GH). VII REGIÓN (MAULE): *Curicó*, Cajón del Azufre, *Albert in 1891* (SGO); 20 km oeste del Paso Vergara, *Calderón in 1967* (CONC); Laguna de Teno, 2,500 m, *Marticorena & Matthei 841* (CONC). *Linares*, Cordillera de Linares, *Philippi in 1862* (G, HAL, S); Termas de Longaví, *Schumann in 1888* (SGO). *Talca*, Laguna del Maule, *Aravena 1021* (UC), *Ricardi et al. 969* (CONC, MO). VIII REGIÓN (BÍO-BÍO): *Bío-Bío*, Cordillera de Antuco, La Cueva, *Rahmer in 1887* (SGO). *Ñuble*, Termas de Chillán, *Jaffuel 3728* (GH), *Pennell 12413* (F, GH, NY, PH), *Solomon 4372* (MO). IX REGIÓN (ARAUCANÍA): *Malleco*, Termas del Río Blanco, 1,300 m, 38°35′S, 71°35′W, *Solomon 4504* (MO). XII REGIÓN (MAGALLANES): *Última Esperanza*, Estancia Cerro Paine, 50°59′S, 72°58′W, *Pisano 4344* (HIP, MO).

Epilobium nivale is a distinctive, high montane species, readily recognized by its glabrous, delicate, decumbent, clumped or somewhat caespitose stems, with few, small pink flowers. Only *E. glaucum* and some individuals of the introduced *E. paniculatum* are also glabrous, but they are much more robust and erect. The small pink flowers are often functionally cleistogamous, because they open partially or not at all on cloudy days, and only for a few morning hours on sunny days.

Epilobium nivale grows sympatrically with four other species, but only rarely is there evidence to suggest interspecific hybridization. Hybrids with *E. australe* and *E. densifolium* would be difficult to distinguish from small-leaved forms of those species, except perhaps in flower size. Recognizable hybrids involving *E.*

ciliatum have not been found, and only a single collection from Termas de Chillán, Prov. Ñuble, Chile (*Solomon 4372,* MO) exhibits a tendency toward larger, acuminate leaves and the more erect stems characteristic of *E. glaucum*. This specimen, however, had a pollen stainability of 96%, which is substantially different than the stainability of artificial hybrids between these species.

Ecologically, *E. nivale* occurs in the same habitats and community associations in the southernmost disjunct populations as it does in, for example, the vicinity of Lago Nahuel Huapi; that is, in wet places at the upper limits of *Nothofagus pumilio* (Poepp. & Endl.) Krasser scrub and at higher elevations. In the Torres del Paine region, at elevations approaching 1,000 m, *E. nivale* is apparently the only species found in permanently wet places (*Pisano,* 1974, as *E. conjungens*). Farther north, beyond the limits of the *Nothofagus* forest, *E. nivale* continues to appear in permanently wet sites, but at increasing elevations.

7. **Epilobium barbeyanum** H. Lév., Bull. Herb. Boissier, sér. 2, 7:589. 1907. TYPE: Chile, IV Región (Coquimbo), Vegas del Toro, Cordillera de Coquimbo, 2,500 m, 1 February 1883, *F. Philippi* (?) (G, holotype, photograph MO; JE, SGO-53122, isotypes). The specimen at G is accompanied by a letter from F. Philippi dated 29 May 1883, and the specimens were probably collected by him. H. Lév., Repert. Spec. Nov. 9:19. 1910–11. Samuelsson, Svensk Bot. Tidskr. 17:265. 1923; Svensk Bot. Tidskr. 24:4. 1930.

Perennial herbs (8–)15–40 cm tall, overwintering and reproducing vegetatively by elongate leafy shoots or soboles produced from the base. Stems erect ascendent or decumbent, terete, usually simple or sparingly branched throughout, abundantly branched from the base, densely pubescent throughout with erect glandular hairs, 0.1–0.2 mm long, with an admixture of strigillose hairs, 0.1–0.2 mm long, in descending lines from the petiole bases or scattered in the inflorescence. Leaves mostly opposite, usually alternate in the inflorescence, the internodes often elongate and the leaves remote in fruit, thin, bright green, lanceolate to narrowly ovate, (0.6–)1–2 cm long, 0.2–1 cm wide, acute to acuminate, rarely obtuse at the apex, remotely denticulate with 3–5 teeth on each side, the margin frequently undulate, acute to obtuse or occasionally rounded at the base, with erect glandular hairs on both surfaces, usually with an admixture of strigillose hairs on the adaxial midrib and margins or thinly scattered on both surfaces, glabrate with age, the lateral veins obscure, 2–4 on each side of the midrib, on poorly defined petioles 0–1 mm long. Inflorescence erect, simple, the leaves subtending the flowers undifferentiated or slightly reduced in size. Flowers erect. Ovaries densely covered with erect glandular hairs, with an admixture of strigillose hairs, these also often dense, 0.9–1.5 cm long on pedicels 1–5 mm long. Floral tube 0.8–1.5 mm deep, 1.3–2(–2.7) mm across, externally with erect glandular and scattered strigillose hairs, internally with a conspicuous ring of erect villous hairs, 0.15–0.2 mm long near the base. Sepals lanceolate, 2.5–3.2(–4) mm long, 0.9–1.5 mm wide, with erect glandular and scattered strigillose hairs. Petals pale pink, obovate, 4–6 mm long, 2.5–3.4 mm wide, the notch 1–1.7 mm deep. Anthers cream to white, 0.6–1 mm long, 0.5–0.7 mm wide; filaments cream to white, those of the longer stamens 1.5–2(–3) mm long, those of the shorter 0.6–

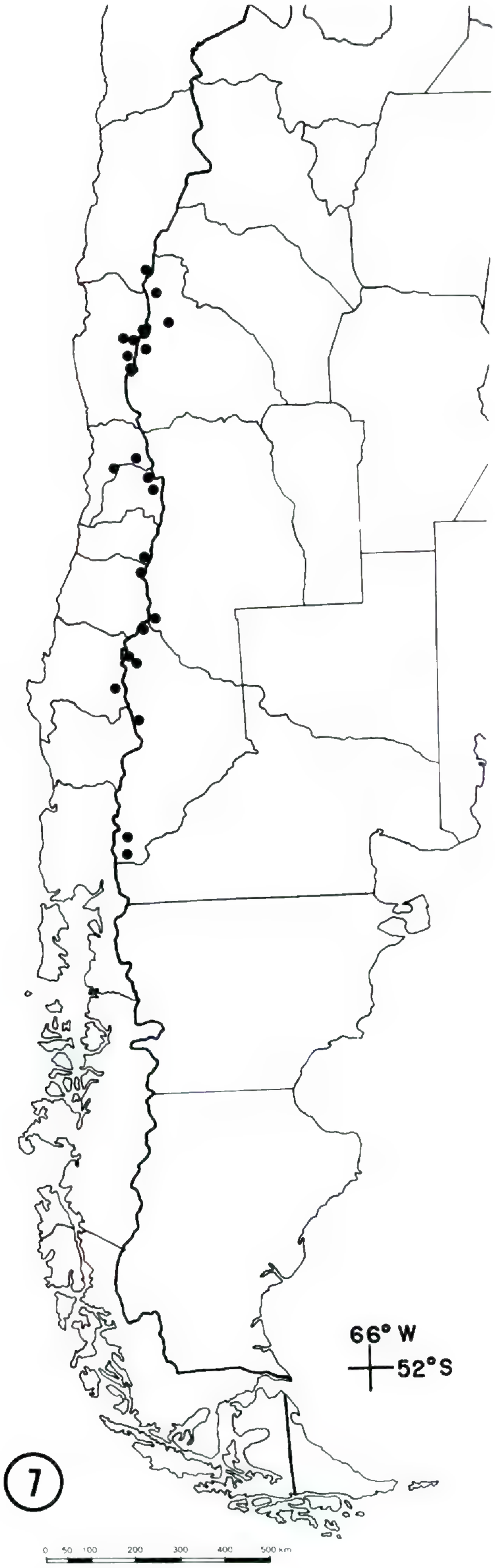
1(–1.9) mm long; the longer stamens shedding directly on the stigma at or shortly after anthesis, occasionally the shorter ones also. Style cream to white, capitate, 0.6–1 mm long, 0.6–1 mm thick. Capsules strictly erect, sparsely covered with erect glandular and scattered strigillose hairs, 3.4–5.2 cm long, 1.3–1.6 mm thick, on pedicels (0.5–)1.2–2.9 cm long. Seeds brown, papillose, obovoid, 0.85–1.3 mm long, 0.4–0.5 mm thick; coma white to slightly yellowish brown, 5–8 mm long. Gametic chromosome number, $n = 18$.

Distribution (Fig. 7): In very wet places in bogs, and along streams, sometimes partially submerged or floating; throughout the central Andes of Chile and Argentina, from southern III Región (Atacama), Chile, and central San Juan Prov., Argentina, southward to the vicinity of Lago Nahuel Huapi; also in the coast range (Cuesta La Dormida) between Santiago and Valparaíso, at elevations of 2,000–3,500 m in the north, gradually descending to 900–1,700 m in the southern part of its range. Flowering November to March.

Specimens examined: ARGENTINA, MENDOZA: Dpto. Malargüe, camino a Paso Pehuenches, Km 50, 1,800 m, *Cabrera et al. 22831* (LP). NEUQUÉN: Dpto. Los Lagos, Estancia Fortín Chacabuco, *Boelcke 4547* (BAA); Dpto. Minas, Arroyo Las Bandurria, entre Las Ovejas y Laguna Epulauquén, 1,250 m, 36°55′S, 70°56′W, *Boelcke et al. 10788* (BAA, BAB, MO), *Ragonese 225* (BA, RSA); Dpto. Minas, Laguna Epulauquén, 1,300 m, 36°50′S, 71°05′W, *Boelcke 10906* (BAA, BAB, MO); Dpto. Chos Malal, Vegas del Pelán, 1,700 m, 36°54′S, 70°20′W, *Boelcke et al. 11134* (BAA, BAB, MO); Dpto. Minas, Laguna Varvarco Campos, Arroyo Benítez, 36°17′S, 70°39′W, *Boelcke 14224* (BAA, BAB); Traful, Estancia La Primavera, *Castellanos in 1938* (BA, RSA), *Gerrovía in 1938* (LIL); Rahue, camino a Aluminé, *Dawson & Schwabe 2180* (BAA, BAB, CTES); Paso Pino Hachado, *Hauman in 1920* (BA); Dpto. Loncopué, Cajón Chenque-Pehuén, 38°06′S, 70°55′W, *Rugolo & Agrasar 172* (BAA, MO). SAN JUAN: Dpto. Calingasta, Manantiales, 3,500 m, *Fabris & Zuloaga 8449* (LP), *Zardini 180* (LP); Dpto. Iglesia, Río Blanco, Sierra San Guillermo, 3,200 m, 29°08′S, 69°30′W, *Hosseus 1443* (CORD); Dpto. Calingasta, Cienaga de Las Cabeceras, 2,700 m, 31°47′S, 69°07′W, *Kurtz 9806* (BAF, CORD), *9815a* (CORD), *Spegazzini in 1937* (BAB); Dpto. Iglesia, Tudcum, *Perrone in 1950* (BA, MO).

CHILE, III REGIÓN (ATACAMA): *Huasco,* Quebrada Alfalfa, 2,800 m, 28°52′S, 69°49′W, *Johnston 5996* (GH, S); Río de la Laguna Grande, 2,750 m, 28°44′S, 69°57′W, *Johnston 6009* (GH, S). IV REGIÓN (COQUIMBO): *Choapa,* Río Illapel, *without collector or date* (K), *Volkmann in 1860–61* (SGO); Quebrada La Vega Escondida, E of Cuncumén, 2,630 m, *Morrison & Wagenknecht 17433* (GH, NA, UC), *Worth & Morrison 16556* (NA, UC). *Elqui,* Laguna de Elqui, *Barros 6616* (US); 6 km al oeste del Embalse La Laguna, 3,100 m, 30°13′S, 70°04′W, *Ricardi et al. 1792* (CONC). *Limarí,* La Hualtata, 2,500 m, 30°39′S, 70°39′W, *Jiles 1182* (CONC); Río Molles, 2,600 m, 30°44′S, 70°36′W, *Jiles 1966* (CONC), *Jiles 2098* (CONC); Río Flamencos, 2,700 m, 30°40′S, 70°23′W, *Jiles 2914* (CONC); Potrero Grande, 2,700 m, 31°18′S, 70°50′W, *Jiles 4837* (CONC). V REGIÓN (ACONCAGUA): *Los Andes,* Hacienda San Vicente, 2,000 m, 32°54′S, 70°37′W, *Martínez in 1968–69* (SGO). REGIÓN METROPOLITANA (SANTIAGO): *Cordillera,* Cordillera de Santiago, *Philippi* (G, mixed with *E. ciliatum*); El Refugio, on road to Lagunillas, 2,100 m, 33°40′S, 70°20′W, *Solomon 4295* (MO), *4296* (MO). *Melipilla,* 3 km S of Las Vizcachas, La Dormida, *Morrison & Wagenknecht 17110* (GH, UC). *Santiago,* Entre Maitenes y Pérez Caldera, 2,000 m, 33°11′S, 70°29′W, *Skottsberg & Sparre 11063* (CONC, H, S); Road to Farellones, 2,050 m, 33°20′S, 70°18′W, *Solomon 4285* (MO), *4360* (MO); Farellones, 2,200 m, *Wall & Sparre in 1947* (S). VI REGIÓN (O'HIGGINS): *Colchagua,* 25 km above La Rufina, road to Termas Vegas del Flaco, 1,450 m, 34°55′S, 70°30′W, *Solomon 4320* (MO). VII REGIÓN (MAULE): *Curicó,* Cordillera del Planchón, *Née in 1793* (MA). VIII REGIÓN (BÍO-BÍO): *Bío-Bío,* Andes de Antuco, *Poeppig in 1828* (M, OXF; mixed with *E. australe*); Road to Laguna La Laja, 930 m, 37°25′S, 71°25′W, *Solomon 4444* (MO). *Ñuble,* Cuchacucha, *Philippi* (JE).

Epilobium barbeyanum is most distinctive due to its dense, erect glandular pubescence throughout, the sparsely toothed, often undulate leaf margins, and the usually elongate leafy basal shoots. Only some populations of *E. ciliatum* and *E. denticulatum* are as densely glandular, but they have distinctive features, such as turions or spreading pubescence. Superficially, *E. barbeyanum* may resemble *E. australe* in leaf shape and habit but generally the leaves are more lanceolate,



FIGURES 7–8. Distribution of *Epilobium species*.—7. *E. barbeyanum*.—8. *E. densifolium*.

and *E. australe* completely lacks glandular pubescence. The elongate basal shoots (up to 25 cm long) are a result of growth in water-saturated or mucky soils in boggy places. In slightly drier situations at the edges of wet places, the plants may be much smaller and produce few or no basal shoots. The shoots and main stems are frequently densely intertwined, and often found floating or partly submerged, with the erect flowering portions elevated above the soil or water surface.

Hector Léveillé first described *Epilobium barbeyanum* while reviewing the epilobiums in Herbiers Boissier and Barbey-Boissier (Léveillé, 1907). His original description was very short and generalized enough that it would have been suitable for several species. Four years later, he published an amplified diagnosis of the single collection with which he was acquainted, citing for the first time the type locality (Léveillé, 1911).

Epilobium barbeyanum grows sympatrically with several species and occasionally forms hybrids. Plants clearly of hybrid origin between *E. barbeyanum* and *E. glaucum* have been collected from La Hierba Loca (Prov. Limarí, Chile, *Jiles 4214*, CONC; pollen stainability 35%). Two probable hybrids with *E. ciliatum* have also been seen, one from Las Cabeceras, Dpto. Calingasta, Prov. San Juan, Argentina, *Spegazzini in 1937* (BAB), the other from Cerro Vizcachas, in the coast range between Santiago and Valparaíso, Chile, *Schlegel 4987* (CONC; pollen stainability 47%). These hybrids are characterized by reduced seed set and pollen fertility, and an intermediate morphology most strongly reflected in the growth habit, leaf shape, and venation.

8. Epilobium densifolium Hausskn., Monogr. *Epilobium* 256, *tab. 18, f. 77a–b.* 1884. TYPE: "Chile bor. Andes, ad nives perpetuas," without more precise locality, 1828, *E. Poeppig* (LE, holotype, not seen; JE, PR, UPS, isotypes). Probably from the Andes near Volcán Antuco, where Poeppig collected extensively from November 1828 to early February 1829, although it cannot be definitely ruled out that the specimens could have been taken from the Andes above San Felipe, Los Andes Prov., during the first week of January 1828 on Poeppig's return from Mendoza (Urban, 1896). Reiche, Fl. Chile 2:244. 1898.

E. pauciflorum R. Phil., Anal. Univ. Chile 84:748. 1893, non Schrank, Denskschr. Königl.-Baier. Bot. Ges. Regensburg 1(2):15. 1818, nec Dulac, Fl. Haute-Pyr. 332. 1867. TYPE: Chile, VIII Región (Bío-Bío), Prov. Bío-Bío, Cordillera de Antuco, La Cueva, January 1887, *C. Rahmer* (SGO-41441, lectotype here designated, photograph MO; JE, isolectotype). Samuelsson, Svensk Bot. Tidskr. 17: 260. 1923; Svensk Bot. Tidskr. 24:11. 1930.

E. lignosum F. Phil., Anal. Univ. Chile 84:746. 1893. *E. nivale* var. *lignosum* (F. Phil.) Hosseus, Trab. Inst. Bot. Farm., Buenos Aires 33:56. 1915. TYPE: Chile, VII Región (Maule), Prov. Curicó, Cuesta de Las Animas, 35°29′S, 70°52′W, 15 February 1879, *F. Philippi* (SGO-41440, lectotype here designated, photograph MO, drawing JE; SGO-53101, probable isolectotype, photograph MO). H. Lév., Iconogr. *Epilobium, tab. 196.* 1911.

Caespitose, clumped perennial herb, 10–25(–35) cm tall, usually with a long, contorted, more or less woody rootstock. Stems ascendent, numerous, simple, or occasionally few branched above, terete, strigillose throughout, with hairs 0.1–0.2 mm long, or glabrate below, then the pubescence mostly limited to descending lines from the petiole bases, densely leafy, often with fascicles of small leaves in the axils of stem leaves. Leaves mostly opposite, alternate only in the inflorescence, thick, green, occasionally glaucous, narrowly lanceolate to lanceolate,

0.5–2.4 cm long, 1.5–6 mm wide, acuminate or acute at the apex, subentire or remotely denticulate, with 1–3(–5) teeth on each side, acute to cuneate at the base, strigillose on both surfaces, or glabrate with age and then strigillose on the margins and the adaxial midrib, the lateral veins obscure, 2–3 on each side of the midrib, on poorly defined petioles 0–1.5 mm long. Inflorescence erect, simple, few-flowered, the leaves subtending the flowers only slightly, if at all, reduced in size. Flowers erect. Ovaries occasionally reddish, strigillose, 0.8–2 cm long, on pedicels (0.3–)0.5–1(–1.5) cm long. Floral tube 1.4–2.2 mm deep, 2–3 mm across, externally strigillose, internally with a ring of erect villous hairs 0.1–0.15 mm long near the base, rarely glabrous. Sepals lanceolate (4.2–)5–7.3 mm long, 1.2–2 mm wide, slightly keeled at the base, strigillose. Petals pale pink to rose purple, often the base of the petal paler than the apex, obovate, rarely broadly so, 7–12 mm long, 4–6(–7.5) mm wide, the notch (1.2–)2.3–3.2 mm deep. Anthers cream, 1–1.7 mm long, 0.5–0.8 mm wide; filaments cream, those of the longer stamens 2.2–3.5 mm long, those of the shorter 1.3–2.4 mm long; the anthers usually held away from the stigma at anthesis, usually the longer stamens bending and barely shedding on the lower part of the stigma after anthesis. Style cream, (2.2–)3.8–5.5 (–7) mm long, occasionally with a few villous hairs toward the base; stigma cream, clavate, 1.1–2 mm long, 0.7–1.2 mm thick, occasionally exserted beyond the longer stamens. Capsules erect, sparsely strigillose, 2.5–4.2 cm long, 1.5–2 mm thick on pedicels 0.6–1.7(–2.5) cm long. Seeds brown, papillose, obovoid, 1.4–1.9 mm long, 0.5–0.65 mm thick; coma white to slightly yellowish, 4–7 mm long.

Distribution (Fig. 8): On rocky, stable scree, or rocky stream banks, near or above timberline, or extending to lower elevations along gravelly stream beds, or on volcanic cinders. Central Andes of Chile and Argentina, from Paso Portillo (33°S), southward along the mountains to the vicinity of Lago Puelo, Chubut Prov., Argentina, usually between 1,200–2,700 m, rarely as low as 800 m. Flowering late December to early March.

Specimens examined: ARGENTINA, CHUBUT: Lago Puelo, *Pérez-Moreau in 1941* (BA, RSA). NEUQUÉN: Parque Nacional Nahuel Huapi, Refugio Cerro Colorado, *Boelcke 6900* (BAA, BAB, MO), *de la Sota 2245* (LIL); Parque Nacional Nahuel Huapi, filo entre Cerro Angostura y Cerro Mojón, *Boelcke & Correa 7115* (BAA, BAB); Dpto. Minas, Paso del Macho, 2,280 m, 36°26′S, 70°46′W, *Boelcke et al. 13905* (BAA, BAB, MO), *13915* (BAA, BAB, MO); Dpto. Lácar, Cerro Chapelco, 40°14′S, 71°16′W, *Cabrera 20532* (LP), *Correa et al. 5908* (BAB); Parque Nacional Lanín, Arroyo Rucu-leufú, *Correa et al. 5663* (BAB, MO); Ridge to Mt. O'Connor, *Diem 3600* (MO); Parque Nacional Lanín, Cerro Malo, *Dimitri et al. in 1963* (BAB), *León & Calderon 1328* (BAA, MO); *Schajovskoy in 1968* (LP); Faldeos del Volcán Lanín, 1,600 m, *Gentili 533* (CTES); Lago Nahuel Huapi, Río Huemul, 770 m, *Ljunger 766* (GB); Lago Nahuel Huapi, Cordón del Colorado, Cerro de la Curva, *Pérez-Moreau in 1940* (BA, MO, RSA). RÍO NEGRO: Cerro Tronador, *Cabrera & Crisci 19231* (LP); *Castagnet 83* (LP), *Dimitri et al. in 1964* (BAB), *Gentili in 1975* (MO), *Maldonado 261* (GH, LP); *Solomon 4638* (MO); Cerro V. López, W of Bariloche, *Fabris 2177* (M), *Solomon 4618* (MO); Cerro Catedral, *Fabris 2233* (LP, M); Cerro Goye, 41°07′S, 71°30′W, *Hosseus 263* (CORD); Parque Nacional Nahuel Huapi, Cerro Riggi, *Marchionni 222* (LP); Lago Frías, camino al Ventisquero Frías, *Montiel in 1946* (LIL), *Pérez-Moreau in 1940* (BA, MO, RSA); E side of Lago Guillermo, 810 m, 41°25′S, 71°28′W, *Solomon 4645* (MO); Parque Nacional Nahuel Huapi, nacimiento del Río Manso, *Vervoorst in 1948* (LIL).

CHILE, V REGIÓN (ACONCAGUA): *Los Andes,* Paso Portillo, 2,700 m, *Wall in 1946* (GB, S). VI REGIÓN (O'HIGGINS): *Cachapoal,* Hacienda de Cauquenes, *Dessauer in 1875* (M); Ventisquero Cipreses, *Dessauer in 1876* (SGO). VII REGIÓN (MAULE): *Curicó,* Las Yeguas, 35°23′S, 70°30′W, *Borchers in 1880* (GOET); Lagunas de Teno, 2,550 m, 35°12′S, 70°30′W, *Mahu 5682* (H); Volcán Peteroa, *Philippi (?) in 1896* (BM). VII REGIÓN (BÍO-BÍO): *Bío-Bío,* Laguna La Laja, *Boelcke et al. in 1969* (BAA, BAB, CTES), *Cabrera 19675* (LP); *Clark & Brown 1393* (ASU, MO); *Solomon 4433* (MO);

Zöllner 6225 (MO, NA), *9370* (MO); Cordillera Araucanía, La Cueva, *Rahmer in 1886* (JE, SGO); Trapa-Trapa, *Rahmer in 1886* (SGO). *Ñuble*, Termas de Chillán, *Jaffuel 2794* (GH), *Pennell 12429* (F, GH, NY, PH, S, US), *Pfister in 1947* (CONC), *Ricardi 5588* (MO). IX REGIÓN (ARAUCANÍA): Without precise locality, *Philippi in 1888* (CORD, K, US, WU). *Malleco*, Termas del Río Blanco, 1,200 m, *Clark & Brown 1407* (ASU, MO), *Klempau in 1972* (VALD), *Montero 3675* (GH), *Pfister in 1948* (CONC); *Solomon 4495* (MO); *4504* (MO); *4506* (MO); Termas de Tolguaca, *Pfister in 1939* (CONC); Volcán Lonquimay, 1,600 m, *Sparre & Constance 10909* (CONC, UC); Paso Lolco, 1,500 m, *Zöllner 6245* (MO); *10209* (MO).

Epilobium densifolium is a strikingly handsome plant with large pink or rose purple flowers, small lanceolate leaves, caespitose habit, and a contorted, often woody rootstock. Some individuals of *E. densifolium* might possibly be confused with smaller leaved plants of *E. australe*, although they can be readily distinguished by the few large flowers, seeds longer than 1.4 mm, and the stem pubescence distributed around the stems throughout.

Epilobium densifolium was described from a single Poeppig collection seen by Haussknecht at Leningrad (LE). Part of the Leningrad material was separated by Haussknecht for his herbarium, now at Jena (JE), and a fragment of that was acquired by Samuelsson, who saw only Haussknecht's specimens. Samuelsson (1923) maintained *E. densifolium* as distinct from *E. pauciflorum* R. Phil. and went so far as to include it in the group Palustriformia, along with *E. puberulum*, based on the lack of raised decurrent lines from the petiole margins. A close examination of the available type specimens, however, shows that there are evident raised lines in the upper portions of the stems. The flowers and seeds of the type are smaller than is typical for the species, but all other morphological features can be easily included in the species as it is circumscribed here.

The name *Epilobium pauciflorum* was proposed only a few years later (Philippi, 1893) for two collections of large-flowered plants from Araucanía, but this name proves to be a later homonym. R. Philippi stated in the description "E. suffruticosum, glaberrimum, humile; . . . ." The specimens cited, however, are not glabrous, but more or less densely strigillose. There is no confusion as to which specimens Philippi was describing from his annotations, so this must have been an accidental error. Most collections have been identified as *E. pauciflorum* primarily because of the uncertain identity and relationship of the type of *E. densifolium*.

Epilobium densifolium occurs in the driest sorts of habitats of any native South American *Epilobium* species, growing in rocky scree, often along stream banks, but frequently on hillsides, and not necessarily associated with running water. In one instance, a large population was found growing in dry, loose cinder scree on the lower slopes of Volcán Antuco (*Solomon 4433*, MO). These plants had the longest, woodiest roots of any collection seen, up to 30 cm long and 5 mm thick.

Of the native species in South America, *E. densifolium* produces the largest flowers and seeds. Only a few populations or individuals of *E. denticulatum* and *E. australe* have flowers that overlap with the lower portion of the size range for *E. densifolium*. Petal color varies from pink to rose purple, often with the distal end of the petal having the darkest shade, fading to white at the proximal end.

Normally at anthesis the anthers are held away from the stigma. Some hours after the flowers open, the longest stamens bend inward and the anthers usually make contact with the lower portion of the clavate stigma. Only rarely is the

stigma fully exserted beyond the longest stamens (Paso Lolco, Prov. Malleco, Chile, *Zöllner 6245,* MO). The result is that in most populations, if the flower is not cross-pollinated, at least some measure of self-pollination will occur.

Because of these features one might expect that hybrids involving *E. densifolium* and other species might be fairly common. This does not appear, however, to be the case, even though *E. densifolium* grows sympatrically with four other species. Only a few collections show intermediate morphological characters that would indicate hybridization in their ancestry, with *E. glaucum* most likely as the other parent. For example, *Dimitri et al. in 1964* (BAB) from Monte Tronador, Río Negro Prov., Argentina, and *Solomon 4495* (MO) from Termas del Río Blanco, Malleco Prov., Chile, both show the long, narrowly acuminate, sparsely toothed leaves of *E. glaucum,* are much more robust and less leafy than is typical for *E. densifolium,* but in other characters are more *E. densifolium*-like. Two other collections, *Solomon 4433* (MO) and *Clark & Brown 1393* (MO), both from populations along the lower slopes of Volcán Antuco, Bío-Bío Prov., Chile, show particularly strong indications of hybrid origin between *E. densifolium* and *E. glaucum,* with reduced pollen stainability (54% and 61%, respectively), as well as intermediate habit and leaf morphology.

Epilobium australe may also be involved in hybridization with *E. densifolium,* but hybrids would probably be difficult to distinguish. One such possible hybrid comes from Volcán Osorno, Osorno Prov., Chile (*Sparre & Constance 10722,* CONC). This collection has the thick, woody rhizomes of *E. densifolium,* the leaves intermediate between the two species, but the narrower capsules and smaller seeds of *E. australe*. Specimens of *E. densifolium* have not been seen from Volcán Osorno, but it does occur within 40 km, while *E. australe* is represented by a number of collections from this area. This odd collection may be only an unusual form of *E. australe,* but it is very unlike any other specimens seen, which suggests a possible hybrid origin.

9. **Epilobium australe** Poeppig & Hausskn. ex Hausskn., Monogr. *Epilobium* 269. 1884. TYPE: Chile, VIII Región (Bío-Bío), Prov. Bío-Bío, Volcán Antuco, February 1829, *E. Poeppig* (W, lectotype here designated, photographs GH, MO; OXF, isolectotype; BR, JE, M, P (photograph GH), PR, W, probable isolectotypes). Reiche, Fl. Chile 2:247. 1898. H. Lév., Iconogr. *Epilobium, tab. 209.* 1911. Samuelsson, Svensk Bot. Tidskr. 17:282. 1923; Svensk Bot. Tidskr. 24: 4. 1930.

E. tetragonum β antarcticum Hook. f., Fl. Antarct. 2:270. 1847. *E. antarcticum* (Hook. f.) Kuntze, Rev. Gen. 3(2):97. 1898. TYPE: Chile, XII Región (Magallanes), Prov. Magallanes, Puerto del Hambre (Port Famine), 53°38′S, 70°56′W, 1827, *P. King* (Commander of the first voyage of the *Adventure & Beagle*) (K, lectotype here designated, photograph MO; BM 2 sheets, E, K, isolectotypes).

E. lechleri R. Phil. & Hausskn, ex Hausskn., Monogr. *Epilobium* 270. 1884. *E. australe* var. *lechleri* (R. Phil. & Hausskn. ex Hausskn.) Samuelsson, Svensk Bot. Tidskr. 17:285. 1923. TYPE: Chile, XII Región (Magallanes), without specific locality, 1865(?), *R. A. Philippi* (W, lectotype here designated, photograph MO; W 2 sheets, isolectotypes; B (destroyed, photographs BH, GH, MO, NA, NY), SGO-53103 (photograph MO), UPS, probable isolectotypes). The date is taken from SGO-53103, which matches the 3 specimens at W in all morphological particulars. Reiche, Fl. Chile 2:248. 1898.

E. lechleri var. *antarcticum* Macloskie, Rep. Princeton Univ. Exped. Patagonia 8(5):609. 1905, non Hausskn., Monogr. *Epilobium* 270. 1884. *E. lechleri* var. *antarcticum* Hausskn. ex Macloskie &

Dusén, Rep. Princeton Univ. Exped. Patagonia, Revision Fl. Patagonica 185. 1914, nom. superfl. TYPE: Chile, XII Región (Magallanes), Prov. Antártica Chilena, Isla Hoste, Orange Harbour, *without date or collector* (presumably collected by the U.S. Exploring Expedition under the command of Charles Wilkes, because these are the only Orange Harbour collections known, February–March 1839). The description and locality information are apparently copies in shortened form from Haussknecht (1884), although Macloskie may have seen specimens at NY where he did some of the work on the *Report*. Since there is no direct or indirect reference to Haussknecht's work at the time of publication, this must be considered a new name. Later Macloskie & Dusén (1914) referred this name to *E. lechleri* var. *antarcticum* Hausskn.

E. australe var. *pumilum* Samuelsson, Svensk Bot. Tidskr. 17:28. 1923. TYPE: Chile, XII Región (Magallanes), Prov. Tierra del Fuego, Sierra Valdivieso, near Paso de Las Lagunas, 800 m, 11 March 1908, *C. Skottsberg 232b* (UPS, lectotype here designated, photograph MO).

E. australe var. *andinum* (R. Phil.) Samuelsson, Svensk Bot. Tidskr. 17:284. 1923. Based on *E. andinum* R. Phil., pro parte. The new combination was based on a Philippi collection at B (destroyed), presumably a specimen of *E. australe* annotated by Philippi as *E. andinum*. Samuelsson's assignment of this specimen as a variety of *E. australe* is probably reliable, since his understanding of *E. australe* was accurate, as indicated by his exsiccatae. I have seen R. Philippi's handwritten annotations of '*E. andinum*' on collections of three different species, *E. ciliatum* subsp. *ciliatum*, *E. australe*, and *E. nivale*. The epithet, *E. andinum*, is most correctly assigned as a synonym of *E. nivale* (*q.v.* for a discussion of this nomenclatural problem).

E. deflexum Samuelsson, Svensk Bot. Tidskr. 17:286, *tab. 5, f. 1.* 1923. TYPE: Chile, XII Región (Magallanes), Prov. Magallanes, banks of Río de Las Minas (Punta Arenas), 16 February 1908, *C. Skottsberg 232* (UPS, lectotype here designated, photographs MO, S; S, isolectotype).

E. interruptum Samuelsson, Svensk Bot. Tidskr. 17:286, *tab. 3, f. 3.* 1923. *E. australe* var. *interruptum* (Samuelsson) Samuelsson, Svensk Bot. Tidskr. 24:8. 1930. TYPE: Argentina, Prov. Chubut, cerca Laga General Paz, 27 January 1901, *G. Gerling 210* (C, lectotype here designated, photographs MO, S; BAF, UPS, Z, isolectotypes).

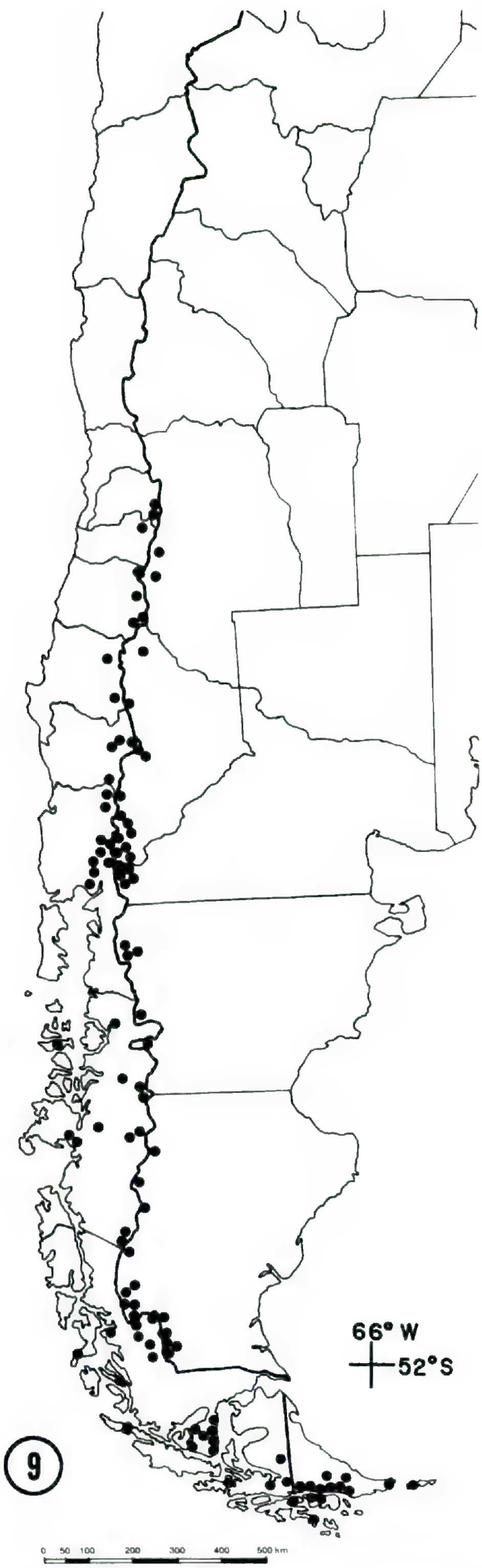
E. transandinum Samuelsson, Svensk Bot. Tidskr. 17:287, *tab. 4, f. 6.* 1923. TYPE: Argentina, Prov. Santa Cruz, Lago Viedma, "in uliginosis," 22 February 1905, *P. dusén 5883* (UPS, lectotype here designated, photographs MO, S; B (destroyed, photographs BH, MO, US), BAF, K, W, isolectotypes).

Clumped perennial herbs, (5–)15–35(–50) cm tall, overwintering and reproducing vegetatively by short rhizomes terminated by leafy shoots or soboles. Rhizome with scale-like leaves, 2–5 mm long, 1–2 mm wide. Stems ascendent, simple, branching generally only from the base, occasionally above, terete, often reddish purple, strigillose, the hairs 0.1–0.2 mm long, in raised descending lines from the decurrent petiole bases, or scattered thinly over the stem surface. Leaves mostly opposite, alternate only in the inflorescence, thick, dull green, often purplish, especially on the margins, narrowly ovate to ovate, rarely broadly so, (0.6–)1–3(–4) cm long, (0.3–)0.6–1.4(–2.2) cm wide, acute to acuminate, rarely obtuse at the apex, remotely, irregularly and coarsely serrate with 4–8(–12) teeth on each side, acute to cuneate, or occasionally rounded to subcordate at the base, strigillose on the adaxial midrib or the upper surface, the lower surface glabrous, the lateral veins prominent, 2–3(–4) on each side of the midrib, on petioles 0–2 mm long. Inflorescence erect, simple. Flowers erect. Ovaries usually reddish purple, strigillose, occasionally densely so, 0.8–1.4 cm long, on pedicels 0–3 mm long. Floral tube reddish purple, 0.4–1.3 mm deep, 1.5–2.7(–3.5) mm across, externally strigillose, internally with a conspicuous ring of erect villous hairs 0.1–0.13 mm long near the base. Sepals often reddish purple, lanceolate, 2.5–4.1 mm long, 1.2–1.7(–2.1) mm wide, slightly keeled at the base, with scattered strigillose hairs along the margins. Petals pale pink, obovate, rarely broadly so, 4–6.2(–9.2) mm long, 2.6–4.5(–7) mm wide, the notch 0.8–1.6(–3.3) mm deep. Anthers cream to white, 0.5–0.8 mm long, 0.3–0.7 mm wide; filaments cream to white, those of the longer stamens 1.5–2.5 mm long, those of the shorter 0.8–1.6 mm long; the

anthers usually held away from the stigma at anthesis, but the longer stamens, and occasionally the shorter, bending and shedding on the stigma after anthesis. Style cream to white, 1.3–3 mm long; stigma cream to white, clavate to capitate, 0.7–1.5(–1.8) mm long, 0.4–1 mm thick. Capsules erect, occasionally deflexed before dehiscence, with scattered strigillose hairs, occasionally glabrous, 3–5 cm long, 1.2–1.7 mm thick, on pedicels 0.3–2.5(–3) cm long. Seeds brown, papillose, obovoid, 1–1.4 mm long, 0.4–0.5 mm thick; coma white to slightly yellowish, 4–7 mm long. Gametic chromosome number, $n = 18$.

Distribution (Fig. 9): Usually inhabiting moist sand or gravel, or growing between rocks along streams or seeps, almost always in or near permanently flowing water. Widely distributed throughout the central and southern Andes of Chile and Argentina, from the upper Valle del Maipo (Cordillera Prov., Chile; 34°S) southward along the mountains to southernmost Tierra del Fuego. In the north, ranging from 2,000–3,700 m, gradually descending southwards to between sea level and 700 m in southern Patagonia and Tierra del Fuego. Flowering (December) January to March.

Representative specimens examined: ARGENTINA, CHUBUT: Dpto. Futaleufú, Esquel, La Hoya, 1,600 m, *Cabrera 23176* (CTES, LP); Dpto. Futaleufú, Lago Futalaufquén, *Soriano 4170* (BAA, MO); Parque Nacional Los Alerces, Lago Verde, *Soriano 4212* (BAA, MO); Lago La Plata, Río Unión, 44°53′S, 71°50′W, *Yplesias & Soetbeer in 1969* (LP). MENDOZA: Antes de llegar al Indigeno, Volcán Overo, 3,700 m, *Lagiglia 2231* (LP); Dpto. Malargüe, Valle Hermoso, *Stuckert 3081* (CORD, mixed with *E. ciliatum*). NEUQUÉN: Cerro Colorado, entre Pto. Manzano y Lago Traful, *Boelcke & Correa 6932* (BAA, BAB); Dpto. Chos Malal, Arroyo de Los Tábanos, 2,330 m, 36°44′S, 70°25′W, *Boelcke et al. 11342* (BAA, MO); San Martín de Los Andes, *S. T. de Burkhart in 1976* (SI); Arroyo Las Lajas, 1,500 m, 38°47′S, 70°42′W, *Comber 287* (E); Dpto. Huiliches, Volcán Lanín, Arroyo Rucu-leufú, *Correa et al. 5596* (BAB, mixed with *E. ciliatum*); Dpto. Lácar, Cerro Chapelco, *Crespo & Giangualani 2079* (BAB, MO); Pino Hachado, *Dawson & Schwabe 2229* (BAA, BAB); Laguna Trolope, 1,700 m, *DeBarba 2017* (BAA, LIL); Paso Puyehue, 1,500 m, *Diem 3604* (MO); Dpto. Lácar, Cerro Malo, 1,700 m, *Hunziker 7006* (BAB); Lago Nahuel Huapi, Río Huemul, 770 m, *Ljungner 765* (GB, MO); Lago Nahuel Huapi, Brazo Rincón, Cerro Dormilón, *Pérez-Moreau in 1940* (BA, LIL, MO, RSA); Volcán Copahue, *Pérez-Moreau in 1941* (BA, MO, RSA); Lago Nahuel Huapi, valle Río Machete, 40°48′S, 71°45′W, *Pérez-Moreau in 1943* (BA, RSA); Parque Nacional Nahuel Huapi, Laguna Frias, *Boelcke & Correa 5372* (BAA, BAB, SI). RÍO NEGRO: Cerro Tronador, entre Mallín Chileno y Refugio, *Boelcke & Correa 5738* (BAA, BAB, SI); Cerro López, 1,700 m, W of Bariloche, *Burkhart 6160* (BA, F, GH, MO, RSA); Cerro Catedral, SW of Bariloche, 1,850 m, *Crespo & Giangualani 2097* (BAB, MO); Parque Nacional Nahuel Huapi, Laguna Los Clavos, *Pedersen 271* (BR, C, P, S, US); Cerro Tronador, *Rubulis in 1976* (MO); Río Llogdconto, 41°22′S, 71°30′W, *Solomon 4629* (MO). SANTA CRUZ: Lago Argentino, Ventisquero Upsala, Cerro Cono, 900 m, *Adam in 1953* (LIL, US); Lago Argentino, Estancia Lago Roca, Cerro Fraile, 760 m, *James 428* (BM, DS, SI); Laguna Fría, 500 m, 50°42′S, 73°03′W, *James 831* (BM, DS); Cerro Mayo, 800 m, 50°22′S, 73°18′W, *James 5036* (BM, DS); Sierra Sangra, Río El Capón, 1,600 m, 48°22′S, 72°21′W, *Kraftsik in 1968* (BAB); Lago de Los Tres, Cerro Fitz Roy, *Luti in 1957* (CORD); Entre Río Geo y Lago Pueyerredón, 600 m, *von Platen & Greiner 121* (BAF, SI, MO, Z); Lago Burmeister, 800 m, *von Platen & Greiner 122* (BAF, SI, MO, Z); Dpto. Argentino, Glaciar Perito Moreno, 190 m, 50°28′S, 73°02′W, *Solomon 4659* (MO); Dpto. Güer Aike, Estancia Achalay, 50°55′S, 72°12′W, *T.B.P.A. (Arroyo et al.) 2349* (HIP, MO, RNG); Dpto. Güer Aike, Estancia Stag River, 410 m, 51°38′S, 71°57′W, *T.B.P.A. (Boelcke et al.) 3132* (BAB, MO); Dpto. Güer Aike, curso superior del Río Turbio, 51°28′S, 72°05′W, *T.B.P.A. (Roig et al.) 3145* (BAB); Dpto. Güer Aike, Estancia La Primavera, 430 m, 51°36′S, 72°17′W, *T.B.P.A. (Ambrosetti & Mendez) 4092* (MO, mixed with *E. ciliatum*); Dpto. Lago Argentino, Lago Viedma, *Witte 24* (BA, BAF, NY, SI). TIERRA DEL FUEGO: Bahía Buen Suceso, 54°47′S, 65°15′W, *Banks & Solander in 1769* (BM, GH, S, US); Almanza, 54°53′S, 67°37′W, *Castellanos in 1932* (BA, MO, RSA); Isla de Los Estados, Bahía Liberty, 54°49′30″S, 64°26′W, *Dudley et al. 1274* (E, MO, RNG, SGO, UC); Near Paso Garibaldi, 330 m, *Goodall 601* (MICH, NA, P, RNG, RSA, UC, US); Estancia Punta Segunda, Río Punta Segunda, *Goodall 1968* (LTR, MICH, MU, NA, UC); Estancia La Correntina near No Kake Mtn., *Goodall 2011* (NA, RNG); Lapataia, edge of Lago Roca, *Goodall 2434* (BAB, NA, RNG); Estancia Cullen, Pampa de Beta, *Goodall 2547* (RNG); Estancia Moat, Río Moat, 54°56′S,



FIGURES 9–10. Distribution of *Epilobium* species.—9. *E. australe*.—10. *E. glaucum*.

66°44′W, *Moore 1686* (MO); Monte Spion-Kop, 54°44′S, 67°18′W, *Moore 2803* (MO); Ushuaia, Arroyo Buena Esperanza, 130 m, *Solomon 4747* (MO).

CHILE, REGIÓN METROPOLITANA (SANTIAGO): *Cordillera,* Valle del Yeso, *Gerling 6088* (BAB, MO; mixed with *E. glaucum*); Los Paramillos, Valle del Maipo, 3,750 m, *Grandjot 3768* (SI, mixed with *E. glaucum*). VI REGIÓN (O'HIGGINS): *Cachapoal,* Río Coya, above El Teniente, 2,900 m, *Pennell 12321* (F, GH, NY, PH, S, SGO, US). VII REGIÓN (MAULE): *Curicó,* Volcán Peteroa, 2,000 m, *Werdermann 599* (BM, CAS, E, F, G, GH, LIL, MO, NY, S, U, UC, US, Z). *Linares,* Cordillera de Linares near Laguna Maule, 2,200 m, *Schlegel 3508* (LA). *Talca,* Laguna del Maule, 2,200 m, *Parra & Rodríguez 189* (CONC). VIII REGIÓN (BÍO-BÍO): *Bío-Bío,* La Cueva, *Rahmer in 1887* (SGO); Laguna La Laja, 930 m, 37°25′S, 71°25′W, *Solomon 4441* (MO). *Ñuble,* Termas de Chillán, 2,100 m, *Pennell 12437* (F, GH, NY, PH, S, SGO, US), 2,200 m, *Werdermann 1314* (BM, CAS, F, G, GH, LIL, MO, SI, U; mixed with *E. ciliatum*). IX REGIÓN (ARAUCANÍA): *Cautín,* Parque Nacional Conguillio, 38°39′S, 71°38′W, *Marticorena et al. 834* (CONC); Volcán Villarrica, entre el Refugio y Pucón, 650 m, *Rojas in 1948* (SGO); Volcán Llaima, 1,350 m, 38°43′S, 71°43′W, *Solomon 4514* (MO). *Malleco,* Paso Pino Hachado, *Merxmüller 25013* (M); Termas del Río Blanco, 1,300 m, 38°35′S, 71°35′W, *Solomon 4498* (MO). X REGIÓN (LOS LAGOS): *Llanquihue,* Puerto Montt, Pangal, *without collector in 1958* (VALD); Cerro Vichadero-Casa Pangue, 1,500 m, 41°05′S, 71°51′W, *Pfister in 1953* (CONC); Volcán Calbuco, Río Aguas Calientes, 41°20′S, 72°37′W, *Rudolph in 1943* (VALD). *Osorno,* Azufreras Volcán Puyehue, 1,350 m, *Rudolph in 1941* (VALD); Volcán Casablanca, Antillanca, 1,000 m, 40°45′S, 72°12′W, *Solomon 4576* (MO); Lago Constancia, 1,000 m, 40°38′S, 71°54′W, *Sparre & Smith 353* (CONC, mixed with *E. ciliatum*). *Valdivia,* Camino de Coñaripe a Puerto Fui, Km 6, *Marticorena et al. 475* (CONC); Volcán Choshuenco, *Moore 344* (LA). XI REGIÓN (AISÉN) *Aisén,* Chonos Archipelago, *Darwin in 1834* (K); Istmo de Ofqui, *Hicken in 1921* (LIL, SI); Golfo San Estebán, Ventisquero San Quentín, 80 m, 46°55′S, 74°05′W, *Hoppe 11* (RNG); E of Puerto Aisén, *Pirión 3394* (GH); Puerto Puyuhuapi, Cerro Tesoro, 900 m, 44°21′S, 72°34′W, *Schwabe 82* (CONC, NY). *Gral. Carrera,* Río Jeinemeni, 30 km S of Lago Buenos Aires, 880 m, *Grosse 23* (CONC, NY); Río Exploradores, Ventisquero Circo, 150 m, 46°20′S, 73°15′W, *Seki 196* (CONC); Lago Buenos Aires, Cerro Pirámide, 1,200 m, *Zöllner 7730* (MO). *Coihaique,* Portezuelo, 800 m, *Behn in 1934* (CONC); Balmaceda, 580 m, *Maldonado 155* (LP). *Capitán Prat,* Peninsula Florida, 1,300 m, 48°40′S, 73°40′W, *Donat 548* (G); Lago San Martín, Estación Ramona, 900 m, *Grosse 56* (LIL, S). XII REGIÓN (MAGALLANES): *Antártica Chilena,* Seno Ponsonby, 220 m, 55°05′S, 68°58′W, *Adams & Andrews-Speed 21* (HIP, RNG); West end of Isla Navarino, *Hicken 62* (BAF); Isla Navarino, NW of Puerto Williams, 400 m, *Moore 359* (LA); Orange Harbour, 55°31′S, 68°03′W, *Wilkes (U.S. Exploring Expedition) in 1839* (K, MO, NY, P, US, JE fragment). *Magallanes,* Puerto Churruca, 53°02′S, 73°56′W, *without collector or date* (E); Seno Otway, Río Caleta, *Cárdenas 21* (HIP, MO); Near Punta Arenas, Cerro Mirador, 670 m, *Dollenz 152* (HIP, MO); Tres Puentes, 200 m, 53°07′S, 70°53′W, *Donat 305* (BA, BAF, BM, CAS, F, GH, K, M, NY, SI, U, Z); 15 km S of Punta Arenas, *Eyerdam et al. 24111* (G, MICH, MO, NA, S, SI, UC, WTU); Cerro Tar, Faro San Isidro, 53°48′S, 70°55′W, *Hernandez 3* (HIP); Port Gallant, 53°40′S, 71°58′W, *Jacquinot in 1841* (P); Punta Arenas, Chabunco, *Magens in 1951* (CONC); Laguna Parrillar, 53°25′S, 71°17′W, *Pisano 3925* (HIP, MO, RNG). *Tierra del Fuego,* Glaciar Reina Isabel II, 54°31′S, 69°15′W, *Pisano 3021* (HIP, MO, RNG); Vicuña, *Ricardi & Matthei 226* (CONC); Fjordo Almirante Martínez, Seno Plüschow, 54°27′S, 70°40′W, *Roivainen in 1929* (BA). *Última Esperanza,* Isla Diego de Almagro, Puerto Pelantaro, 51°24′S, 75°04′W, *Biese 1465* (LIL, SGO); Cerro Prat, 51°29′S, 72°47′W, *Fester in 1931* (SI); Cerro Toro, Sección Lazo, 51°10′S, 72°45′W, *Pisano 4104* (HIP, MO); Estancia La Cumbre, Sierra Baguales, 50°36′S, 72°30′W, *Pisano & Cárdenas 4685* (HIP, MO); Glaciar Grey, 51°00′S, 73°10′W, *Steele 112* (RNG); Peninsula Roca, Seno Resi, 750 m, 51°51′S, 73°02′W, *T.B.P.A. (Pisano) 2923* (BAB, MO); Peel Inlet, 450 m, *Tilman 63* (BM); 0.4 km W of Lago Paine, Río Paine, 150 m, *Williams in 1980* (MO, mixed with *E. glaucum*).

Epilobium australe is quite variable in the size of the plants and the density and size of leaves, but it is readily separable from the other species in South America. Plants usually have mostly opposite, thick, narrowly ovate to ovate leaves with few teeth, the stems first appearing as elongate leafy shoots from short scaly rhizomes, later ascendent, with strigillose pubescence. *Epilobium australe* is most likely to be confused with *E. ciliatum,* but the latter is easily distinguished by its turions, or compact leafy basal rosettes, thin lanceolate leaves with numerous teeth, and the presence of short glandular hairs in the inflorescence.

Plants referable to *Epilobium australe* were first collected by Banks and So-

lander from Tierra del Fuego in 1769. Although Solander gave them a manuscript name, *E. littorale*, the first published name did not appear until 1847 when Hooker described plants acquired by Captain King on the first voyage of the *Adventure* and *Beagle* as a variety of the common and variable European *E. tetragonum*. It was only with Haussknecht's revision of the genus that this distinctive species was given specific recognition (Haussknecht, 1884). Since then, numerous names have been proposed to cover the variations exhibited by *E. australe*, but none of them are distinct enough to warrant recognition based on current evidence, and a number were based on especially trivial characters. For example, *E. deflexum* was based on several plants with nodding inflorescences, a character that has not been seen in any other collections of *E. australe*. What seems most likely is that these plants were pressed in that position, perhaps after being carried through a day's hike in a dark vasculum. The curling of the growing inflorescences when carried in a dark place for some hours is very common; all species of *Epilobium* will do it. Similarly, *E. transandinum* was described because of its larger than average flowers, more rounded seeds and pubescent calyx lobes, all trivial characters when taken in context with the variability normally shown by *E. australe*.

The report of *Epilobium australe* from the Falkland Islands (Haussknecht, 1884) is probably due to a mixing of two separate collections. Three herbarium specimens, labeled as having been collected in the Falkland Islands (Antarctic Expedition, 1839–1843, *J. D. Hooker*, G, K, P), contain pieces of *E. australe* and *E. ciliatum*. The plants of *E. australe* are indistinguishable from those that compose the type material for *E. tetragonum β antarcticum* from Tierra del Fuego and were probably accidentally mixed with specimens of *E. ciliatum* from the Falklands when the material was distributed to other herbaria (cf. Skottsberg, 1913).

One of the most distinctive variants of this species is *Epilobium lechleri*. Haussknecht differentiated this from *E. australe* primarily on the basis of the more coarsely toothed, elongated leaves. These plants tend to be more robust, taller, with larger leaves than most other specimens. A formal taxonomic recognition for them, however, is not useful as plants of this type are found in populations throughout much of the range of *E. australe* and they intergrade continuously with the other plants in those populations. A fine example of this is the series of plants from Orange Harbour, Tierra del Fuego, Chile, collected on the U.S. Exploring Expedition, 1838–1842, in which the plants vary in size from 10 cm to about 40 cm, with small- and large-leaved individuals. Haussknecht identified two plants of the same size from this collection on the same herbarium sheet (K), one as *E. australe*, the other as *E. lechleri*, citing each in the respective protologue. The only differences between the two plants are that the one identified as *E. lechleri* is slightly more robust, with denser foliage composed of leaves with slightly larger teeth, and mature capsules.

There is some geographic basis for the variation seen in plant stature. Larger plants appear with greater frequency from the more southern portion of the species range, but equally large plants are also found much farther north. Superimposed on this geographical variation are elevational and microclimatic factors that also influence the size and leafiness of individual plants. Populations from higher el-

evations are often smaller and more densely leafy (e.g., Cerro Mayo, Santa Cruz Prov., Argentina, *James 5036,* BM, DS; Mt. Wood, Tierra del Fuego, Argentina, *Goodall 3498,* NA). Plants of this habit formed the basis for Samuelsson's *Epilobium australe* var. *pumilum*.

Similarly, exposure and moisture conditions have a profound effect on population variability. This is well illustrated by a series of collections from Volcán Llaima, Cautín Prov., Chile. Plants from a dry, sandy stream bed were low in stature (15 cm), well branched, and densely leafy, with mostly less than 1 cm leaves (*Solomon 4513,* MO); but plants found growing at the edges or in running streams were up to 35 cm tall, sparsely branched, with leaves mostly shorter than the internodes and over 2 cm long (*Solomon 4514, 4516, 4517, 4519,* MO). In addition, those from the drier and warmer sites had mature, dehiscing capsules, while those growing in the cold mountain streams were just beginning to flower. In the same manner, a population from Tierra del Fuego (*Solomon 4747,* MO) produced plants on a seep over rocks in full sun that were 15 to 20 cm tall with graceful stems and small leaves, while only a few meters away on a partially shaded gravel bar, robust plants over 50 cm tall, with large leaves, were common, along with numerous plants of intermediate size.

Ecologically *Epilobium australe* is found most often in rocky sites, especially seeps, or at the edge of rocky mountain streams where there is permanent flowing water, but it can occasionally be found on sand bars or at the edge of bogs. In these habitats it can grow sympatrically with up to five other *Epilobium* species, but only two, *E. ciliatum* and *E. glaucum,* and possibly a third, *E. densifolium,* are known to form hybrids with *E. australe*. Only those involving *E. glaucum* are presented here; the others are discussed under the other two species.

Epilobium australe and *E. glaucum* are broadly sympatric throughout much of their range, although *E. glaucum* extends farther north, while *E. australe* continues farther south. Often both species grow intermixed, and this close association makes occasional hybrids nearly inevitable. From the lower slopes of Volcán Llaima, Cautín Prov., Chile, several plants were collected (*Solomon 4515,* MO) that had intermediate morphology between the two species; glaucous, narrow leaves, and strigillose pubescence throughout. Pollen stainability of this collection was 34%. A second collection from Cerro López, Río Negro Prov., Argentina (*Cordini 188,* S) had similar morphology and poor capsule development.

10. Epilobium glaucum R. Phil., Linnaea 33:70. 1864, non Howell, Bull. Torrey Bot. Club 15:24. 1888. TYPE: Chile, Región Metropolitana (Santiago), Cordillera de Santiago, 1861, *R. A. Philippi* (K, lectotype here designated, photograph MO; G, probable isolectotype). There is a specimen at SGO (53065) that bears two labels. One is in the hand of R. A. Philippi, with the annotation "*Epilobium glaucum* Ph.," from the Cordillera de Los Arañas, January 1861, collected by C. Landbeck. Attached below is a second label in the hand of C. Gay with the following information: "1222. Prov. Coquimbo in humidis andium huertado. Januario 1837." Because of the ambiguous nature of this sheet it has been excluded from consideration, and the lectotype chosen from the other specimens collected, and presumably annotated, prior to the date

of publication. Hausskn., Monogr. *Epilobium* 275. 1884. Reiche, Fl. Chile 2: 250. 1898. H. Lév., Iconogr. *Epilobium, tab. 182*. 1911. Samuelsson, Svensk Bot. Tidskr. 17:289. 1923. Dimitri, Región Bosques Andino-Patagonicos, *tab. 63*. 1972.

E. pedicellare auct. non Presl: Hook. & Arn., Bot. Misc. 3:309. 1833, pro parte.

E. mexicanum auct. non DC.: Walp., Nov. Act. Acad. Caes. Leopold. 19, Suppl. 1:328. 1843.

E. nubigenum R. Phil., Linnaea 33:71. 1864. TYPE: Chile, VIII Región (Bío-Bío), Prov. Ñuble, Baños de Chillán, 26 February 1862, *R. A. Philippi*. There is a mounted label on SGO-53071 in the hand of R. A. Philippi, but without an accompanying specimen, which bears the annotation "*Epilobium glaucum* var. *nubigenum* Ph." An additional annotation by C. Muñoz, February 1946 states, "Ejemplar extraviado, etiqueta junta a *E. glaucum* Ph." Reiche indicated that the specimens were lost at some point prior to his treatment of *Epilobium* in 1898 (Reiche, 1898). Based on the Latin description and the use of the epithet "*nubigenum*" as a variety of *E. glaucum* on the label, the placement of the name *E. nubigenum* as a synonym of *E. glaucum* is probably correct.

E. ramosum R. Phil., Anal. Univ. Chile 84:747. 1893, non Huds., Fl. Angl. 141. 1762. TYPE: Chile, VIII Región (Bío-Bío), Prov. Bío-Bío, Cordillera de Antuco, La Cueva, February 1887, *C. Rahmer* (SGO-41444, lectotype here designated, photographs GH, MO; SGO-53015, isolectotype, photograph MO). H. Lév., Iconogr. *Epilobium, tab. 195*. 1911.

E. patagonicum Rendle, Journ. Bot. 42:367. 1904. TYPE: Argentina, Prov. Santa Cruz, Lago Argentino, Punta Bandera, lower slopes of Mt. Buenos Aires, February–March 1901, *H. Prichard* (BM, holotype, photograph MO).

E. glaucum var. *stenophyllum* Macloskie & Dusén, Rep. Princeton Univ. Exped. Patagonia, Revision Fl. Patagonica, Suppl. 185. 1914. TYPE: Argentina, Territory of Neuquén, northern Patagonia. No authentic material has been seen. Based on *E. glaucum* f. "*stenophylla*" Hausskn., Monogr. *Epilobium* 276. 1884.

Robust, loosely rhizomatous, perennial herbs, (15–)20–70(–100) cm tall, overwintering and reproducing vegetatively by scaly rhizomes terminated by elongate leafy shoots or soboles produced from near the base. Rhizome elongate, 5–20 cm long, with mostly opposite scale-like leaves, 2–6 mm long, 1–3 mm wide. Stems erect or ascendent, often clumped, simple, or sparingly branched above, to densely branched throughout, quadrangular or terete, reddish to purplish brown, glabrous, glaucous, with raised decurrent lines from the petiole bases. Leaves mostly opposite, alternate above or only in the inflorescence, rarely ternate, thick, green, glaucous, sometimes reddish, often with fascicles of small leaves in the axils, narrowly lanceolate, rarely broadly so, 1–4.1(–5) cm long, 0.2–1.2 cm wide, acuminate at the apex, remotely and coarsely denticulate with 2–7 teeth on each side, acuminate to cuneate, or acute, at the base, the lateral veins obscure, 1–3 on each side of the midrib, on poorly defined petioles 0–2 mm long. Inflorescence erect, simple, or occasionally branched, the floral leaves slightly if at all reduced. Flowers erect. Ovaries often reddish purple, glabrous, glaucous, 1.3–3.1 cm long, on pedicels 0.3–1(–1.5) cm long. Floral tube often reddish purple, glabrous, 0.8–1.9 mm deep, 1.5–2.1 mm across. Sepals often reddish purple, lanceolate, 3–5.2 mm long, 1–1.5 mm wide, glabrous. Petals pale pink, obovate, rarely broadly so, 4.2–7(–9) mm long, 2.4–4(–5) mm wide, the notch (0.7–)1.2–2.1 mm deep. Anthers cream to white, 0.9–1.1 mm long, 0.4–0.6 mm wide; filaments cream to white, those of the longer stamens 1.8–3.2 mm long, those of the shorter 1–1.7 mm long; usually the longer, and occasionally the shorter, stamens shedding directly on the stigma at or shortly after anthesis. Style cream to white, 3–4.9(–5.7) mm long; stigma cream to white, clavate, 0.9–1.9 mm long, 0.5–0.7 mm thick, rarely exserted beyond the anthers. Capsules erect, glabrous, 3.5–6 cm long, 1.2–1.6 mm thick,

on pedicels 0.5–1.8(–2.2) cm long. Seeds brown, papillose, obovoid, 1–1.3 mm long, 0.4–0.5 mm thick; coma white or slightly yellowish, 4.5–7 mm long. Gametic chromosome number, $n = 18$.

Distribution (Fig. 10): Common in moist sand, gravel, and among rocks along streams or seeps, embankments, roadsides, or other open, more or less permanently moist situations. Throughout the central and southern Andes of Chile and Argentina, from southern IV Región (Limarí Prov.), Chile, and San Juan Prov., Argentina, southward along the mountains to the vicinity of Torres del Paine and Puerto Natales, Chile. In the northern part of its range found typically from 1,900 to 3,000 m, descending gradually to 150–900 m at its southern limit. Flowering December to March.

Representative specimens examined: ARGENTINA, CHUBUT: Dpto. Cushamén, 30–40 km NE of Esquel, 42°49′S, 71°05′W, *Boelcke et al. 16034* (BAA, BAB, MO); Los Rapidos, Río Futaleufú, *Castellanos in 1945* (BAB, F, LIL); Río Pico, 44°10′S, 71°18′W, *Fablet in 1913* (BAB); Valle de Las Plumas, Lago General Paz, *Gerling 64* (BAF, Z); Río Pico, *Gerling in 1903* (SI); Región del Lago General Pico, 650 m, 44°05′S, 70°55′W, *Hazbera in 1902* (BAB, S, SI); Cholila, *Illin 129* (BAF, BR, CORD, SI); Carrenleufú, 43°50′S, 72°59′W, *Illin in 1900* (LP); Arroyo del Gato, Lago Fontana, 44°56′S, 71°30′W, *Koslowsky in 1896* (LP); Valle de la Laguna Blanca, 45°52′S, 71°15′W, *Koslowsky 80* (CORD, LIL, SI, Z); Camino de Corcovado a Tecka, *Krapovickas 4092* (BAB, LIL); Corintos, orillas del Río Corintos, 43°09′S, 71°35′W, *Lahitte in 1936* (BAB); Dpto. Lanquiñeo, Arroyo Caquel, camino Tecka a Gobernador Costa, 43°22′S, 70°53′W, *Nicora 7510* (BAA, MO); Lago Epuyén, *Soriano 1375* (BAA, CTES, SI). MENDOZA: Dpto. Lujan, Chacras de Coria, 33°00′S, 68°52′W, *Araque 1240* (LIL); Dpto. Las Heras, Estación Polvoredas, 1,850 m, *Cuezzo & Balegno 1871* (LIL); Los Hoyos, 32°46′S, 69°23′W, *Gerth 98* (SI); San Rafael, Los Molles, *Kurtz 7551* (CORD, JE); Rincón de Los Arenales, entre el Paso de Portillo y La Laguna de Diamante, *Kurtz 10979* (CORD); Dpto. Malargüe, Valle Hermoso, 2,900 m, 35°08′S, 70°14′W, *Lagiglia 691* (LP); Dpto. Tunuyan, Valle del Alto Tunuyan, cerca Real de Contreras, *Leal 2124* (LIL, POM); Dpto. San Rafael, Río Grande, Minacar, 2,500 m, *Lourteg 7-94* (LIL, UC); Puente del Inca, *Malme 2935* (GH, LD, MO, S, UPS); Las Heras, Quebrada de Santa María, 2,600 m, 32°48′S, 69°51′W, *Palacios & Barkley 20MZ318* (NY, P, W); Dpto. San Rafael, Los Morros, *Rossi 296* (LIL); Valle del Atuel, Cajón del Burro, 2,700 m, *Wilczek 417* (G, US); Valle del Atuel, Arroyo Manga, *Wilczek 419* (G). NEUQUÉN: Confluencia Traful, *DeBarba 2083* (LIL); Río Malleo, Lago Tromén, 1,000 m, 39°30′S, 71°22′W, *Böcher et al. 1792* (DS); Dpto. Aluminé, Quillén, Estancia La Ofelia, *Boelcke 5174* (BAA, MO); Dpto. Minas, Laguna Epulauquén, 36°50′S, 71°07′W, *Boelcke et al. 10908* (BAA, BAB, MO); Dpto. Minas, Valle del Río Pichi-Neuquén, puesto de Gendarmeria, 36°36′S, 70°49′W, *Boelcke et al. 13631* (BAA, BAB); Dpto. Minas, Laguna Varvarco Campos, Arroyo Benítez, 36°17′S, 70°39′W, *Boelcke et al. 14200* (BAA, BAB, MO); Lago Huechulafquén, 39°46′S, 71°28′W, *Bridarolli 2109* (LP); Lago Nahuel Huapi, Brazo Blest, Arroyo Bravo, *Castellanos in 1938* (BA); Arroyo Las Lajitas, 38°31′S, 70°23′W, *Comber 295* (K); Lago Nahuel Huapi, Isla Victoría, *Cordini 79* (GH, S, US); Dpto. Lácar, Cerro Chapelco, 1,800 m, 40°14′S, 71°16′W, *Crespo & Giangualani 2074* (BAB, MO); Río Bonito, between Puerto Manzano and Villa La Angostura, 800 m, *Diem 3612* (MO); Dpto. Catán-Lil, Picunches, Cañon de Los Cipreses, 38°32′S, 70°15′W, *Kurtz 6322* (CORD, G, JE); Valle del Malalco, 39°15′S, 71°23′W, *Neger in 1891* (M); Lago Nahuel Huapi, Brazo Huemul, Arroyo Huelta, 40°58′S, 71°22′W, *Solomon 4628* (MO); Paso Pino Hachado, Refugio Militar Coronel Pringles, 1,400 m, *Valla et al. 3092* (BAA, CTES, MO); Lago Nonthué, Arroyo Hua Hum, 40°09′S, 71°39′W, *Valla et al. 3275* (BAA, CTES, MO). RÍO NEGRO: Arroyo Ñireco, 41°08′S, 71°17′W, *DeBarba 44* (A, LIL, NY, UC); Bariloche, 770 m, *Buchtien 1319* (BAF, BP, BREM, E, GH, L, M, PR, S, SI, W, Z); Parque Nacional Nahuel Huapi, Laguna Frías, *Cabrera 6072* (LP); El Bolsón, Río Quemquemtreu, *Correa et al. 4191* (BAA, BAB, MO, UC); Villa Cerro Catedral, 1,030 m, 41°10′S, 71°28′W, *Solomon 4612* (MO); Cerro Tronador, 1,200 m, 41°10′S, 71°53′W, *Solomon 4641* (MO); South end of Lago Guillelmo, 810 m, 41°25′S, 71°28′W, *Solomon 4643* (MO). SAN JUAN: Dpto. Calingasta, oeste de Barreal, El Pachón, 2,200 m, 31°38′S, 69°28′W, *Kiesling & Saenz 1467* (SI); Dpto. Calingasta, Cordillera de Espinazito, La Ciénaga Redonda, 31°40′S, 68°55′W, *Kurtz 9558* (CORD). SANTA CRUZ: Dpto. Lago Buenos Aires, 29 km NW of Perito Moreno, 46°25′S, 71°09′W, *Boelcke et al. 16116* (BAA, BAB, MO); Lago San Martín at river, *Dusén 6081* (H, S, UPS); Dpto. Lago Argentino, 40 km W of Calafate, 270 m, *Eyerdam et al. 24304* (G, GH, MO, NA, SI, UC); Dpto. Lago Argentino, S side of Lago San Martín, 340 m, *Eyerdam et al. 24464* (G, GH, MO, NA, S, SI, UC); Dpto. Lago Argentino, Laguna Fría, 50°42′S, 73°03′W, *James 775* (BM, DS, SI); Entre Río Geo y Lago Pueyerredón, 600 m, *von Platen & Greiner 120* (BAF, MO, SI, Z); Los

Antiguos, 330 m, 46°35′S, 71°26′W, *Roivainen 2585* (H); Dpto. Lago Argentino, Glaciar Perito Moreno, 190 m, 50°28′S, 73°02′W, *Solomon 4657* (MO); Dpto. Güer Aike, Estancia La Primavera, 51°36′S, 72°17′W, *T.B.P.A. (Ambrosetti & Mendez) 4086* (MO); Lago Argentino, Brazo Spegazzini, 50°15′S, 73°18′W, *Vervoorst 4767* (LIL).

CHILE, IV REGIÓN (COQUIMBO): *Choapa,* Illapel, *Geisse in 1912* (Z). *Limarí,* Vegas del Río Torca, 31°03′S, 70°43′W, *Geisse in 1890* (SGO); La Hierba Loca, 2,800 m, 31°25′S, 70°41′W, *Jiles 4214* (CONC). V REGIÓN (ACONCAGUA): Los Andes: Valle del Río Blanco, *Boelcke 2508* (BAA, CTES, MO); Juncal (Ojo de Agua), *Buchtien in 1903* (BAF, BM, BREM, E, L, M, S, SI, US, W), *Pennell 12982* (F, GH, NY, PH, SGO, US), *Poeppig in 1830* (BM, F, G, HAL, MO, P, PR, W); Valle Monos de Agua, Refugio Mono Verde, *Schlegel 2442* (CONC). *Petorca,* Cerro Chache, 18 km E of La Ligua, 1,900 m, *Morrison 17042* (G, NA, UC). REGIÓN METROPOLITANA (SANTIAGO): *Cordillera,* Lo Valdes, Refugio Alemán, *Garaventa 5678* (CONC); Cerro San Pedro Nolasco, 33°48′S, 70°16′W, *Gillies* (E, K); Los Paramillos, Valle del Maipo, 3,750 m, *Grandjot 3768* (SI, mixed with *E. australe*); Valle del Yeso, entre Agua Panimávida y Agua Termal, 2,800 m, *Schlegel 2580* (CONC). *Santiago,* Entre Maitenes y Pérez Caldera, 2,000 m, *Skottsberg & Sparre 11062* (CONC, S); 2 km above Farellones, 2,650 m, 33°20′S, 70°18′W, *Solomon 4356* (MO). VI REGIÓN (O'HIGGINS): *Cachapoal,* Hacienda de Cauquenes, *Dessauer in 1875* (M); Río Coya above El Teniente, 2,900 m, *Pennell 12344* (F, GH, PH, SGO). *Colchagua,* Termas Vegas del Flaco, 1,750 m, *Mahu 9855* (H, MO, UC). VII REGIÓN (MAULE): *Curicó,* Laguna de Teno, *Marticorena et al. 7* (CONC, MO); 19 km al este de Los Queñes, 950 m, *Marticorena & Matthei 798* (MO); Cordillera del Planchón, *Née in 1793* (MA, mixed with *E. ciliatum*). *Linares,* Termas de Longaví, *Castellanos in 1938* (BA). *Talca,* Laguna del Maule, 2,250 m, *Aravena 1016* (UC); Cordillera de Maule, *Germain in 1856–57* (BM, G, K, P, W). VIII REGIÓN (BÍO-BÍO): *Bío-Bío,* Faldeo NW of Volcán Antuco, 1,350 m, *Boelcke et al. 6384* (BAA, BAB); Al interior de Santa Barbara, 37°40′S, 72°02′W, *Gay 1220* (SGO); Camino de Bío-Bío a Copahue, 5 km al este de Pitrillon, 840 m, *Marticorena et al. 951* (CONC); Camino de Bío-Bío a Copahue, 4 km al este de Pitrillon, 770 m, 37°53′S, 71°31′W, *Marticorena et al. 991* (CONC, MO); Baños de Pemehue, 38°03′S, 71°43′W, *Pinto in 1949* (CONC). *Ñuble,* Las Trancas, Purgatorio, 1,200 m, 36°48′S, 71°44′W, *Roivainen in 1929* (H); Termas de Chillán, 2,200 m, *Werdermann 1312* (BM, CAS, E, F, G, GH, LIL, M, MO, NY, S, SI, UC, US, Z). IX REGIÓN (ARAUCANÍA): *Cautín,* Lonquimay, *Burkart 9499* (LIL, SI); Volcán Lanín, *Claude-Joseph 5539* (US); Volcán Llaima, 38°43′S, 71°43′W, *Solomon 4518* (MO); Puente Correntoso, 15 km E of Villarrica, 210 m, 39°16′S, 72°00′W, *Solomon 4537* (MO). *Malleco,* Termas de Tolguaca, 1,080 m, *Gunckel 16362* (US); Buenavista, below Volcán Tolguaca, *Pennell 12817* (F, GH, NY, PH, SGO); Túnel Las Raices, boca Norte, 38°33′S, 71°30′W, *Pfister in 1947* (CONC); Termas del Río Blanco, 1,300 m, 38°35′S, 71°35′W, *Solomon 4503* (MO); Volcán Lonquimay, *Sparre & Constance 10928* (CONC, UC). X REGIÓN (LOS LAGOS): *Llanquihue,* Paso Pérez Rosales, 940 m, *Moore 328* (LA, MO); Camino Ensenada a Ralun, *Pfister in 1948* (CONC). *Valdivia,* Daglipulli, 40°12′S, 72°59′W, *Gay 79* (P); Lago Calafquén, *Marticorena et al. 441* (CONC); Queñi, 40°15′S, 71°50′W, *Philippi(?) in 1887* (SGO); 1 km W of Coñaripe, 39°34′S, 72°00′W, *Solomon 4539* (MO). XI REGIÓN (AISÉN): *Aisén,* E of Puerto Aisén, *Pirión 3413* (GH). *Gral. Carrera,* Cerro Pirámide, cerca Puerto Ibañez, *Zöllner 7730* (NA). *Coihaique,* Río Coihaique, cerca puente hacia Los Leones, *Espinosa in 1934* (SGO); State Forest Manonegra, near Coihaique, *Schlegel 6971* (VALD). XII REGIÓN (MAGALLANES): *Última Esperanza,* Eberhardt, 51°40′S, 72°38′W, *Borge 138* (NY, S); Ventisquero Dickson, 50°48′S, 73°10′W, *Jenkins in 1977* (MO); Between Puesto Grey and Valle Olvidado, 50°56′S, 73°10′W, *Steele 82* (RNG); Casas Viejas, 51°40′S, 72°20′W, *T.B.P.A. (Latour et al.) 1814* (BAB, MO); 0.4 km W of Lago Paine on Río Paine, 130 m, *Williams in 1980* (MO, mixed with *E. australe*).

Epilobium glaucum is one of the most easily distinguished species in South America. The glabrous, glaucous, erect stems and long acuminate, few toothed leaves separate it immediately from all others. Only *E. nivale* is also glabrous, but it is characterized by a decumbent habit with small flowers and generally much smaller leaves.

There is relatively little variation in *Epilobium glaucum*. What does exist is most evident in the size of the leaves and branching pattern. As with many plants of open, sunny habitats, slightly shaded forms often have broader leaves and more lax, elongate stems; for example, *Solomon 4641* (MO) from Monte Tronador, Río Negro Prov., Argentina. Also conspicuous are very narrow-leaved populations from Volcán Llaima (*Solomon 4518,* MO), although plants of this type are widely scattered throughout the range of the species. Occasionally plants with

ternate or quaternate leaves are found (e.g., Volcán Antuco, Bío-Bío Prov., Chile, *Solomon 4435*), but this feature does not characterize populations but only sporadic individuals.

Branching is likewise rather variable. Generally stems are simple, or with one or a few lateral branches produced above or from the base. As the growing season progresses, or if the apex of the central shoot is damaged, plants can produce an abundance of lateral shoots throughout. An extreme example of this is shown by a collection from Cautín Prov., Chile (*Solomon 4537,* MO) which was taken from a single plant about 75 cm tall with five major shoots from the base, each with more than 100 lateral branches.

Each erect stem terminates a scaly, branching rhizome that can be up to several decimeters long. Plants of this sort usually appear solitary or in clusters of a few stems. Frequently, however, the rhizomes are tightly and intricately intertwined so that the many shoots are closely spaced with the entire clump producing a rounded, almost shrub-like appearance.

Epilobium glaucum has a broader elevational and latitudinal amplitude than most other species in temperate South America and is often weedy, occupying the same sorts of habitats as the even more widespread and very weedy *E. ciliatum*. In a fashion similar to many other species of *Epilobium, E. glaucum* prefers open, permanently moist sites, especially in sand or gravel along mountain streams.

With such an extensive range, it is not surprising that *Epilobium glaucum* grows sympatrically with at least seven other species. Apparent hybrids have been seen between *E. glaucum* and at least four of these, *E. ciliatum, E. barbeyanum, E. densifolium,* and *E. australe,* which are discussed in detail under each species.

11. Epilobium hirtigerum A. Cunn., Ann. Nat. Hist. 3:33. 1839. TYPE: New Zealand, North Auckland, skirts of forest on west side of Wangaroa Harbour, 1833, *R. Cunningham* (K, holotype; WELT, isotype). *E. junceum* var. *hirtigerum* (A. Cunn.) Curtis, Stud. Fl. Tas. 2:231. 1963. (Complete synonymy given by Raven & Raven, DSIR Bull. 216:141–144. 1976.)

E. tetragonum auct. non L.: Camb. in St.-Hil., Fl. Bras. Merid. 2:192. 1829. Micheli, Fl. Brasil. 13(2):174. 1875, Arechavaleta, Anal. Museo. Nac. Montevideo 5:92. 1905.

E. junceum sensu Hook. f., Fl. N. Z. 1:60. 1853, pro parte.

E. brasiliense Hausskn. Oesterr. Bot. Z. 29:119. 1879. TYPE: Uruguay, Dpto. Montevideo, "Le long de la Riviera qui passe au Moulin des jesuittes de Monte Video," 1767, *P. Commerson* (P, lectotype, photographs GH, MO; MPU, isolectotype; Raven & Raven, DSIR Bull. 216:141, 1976). Hausskn., Monogr. *Epilobium* 253, *tab. 15, f. 71, 71a.* 1884. C. Bettfreund, Flora Arg. 230, *tab. 140.* 1901. H. Lév., Iconogr. *Epilobium, tab. 190.* 1911. Samuelsson, Svensk Bot. Tidskr. 17: 247. 1923. Munz, Comun. Bot. Mus. Hist. Nat. Montevideo 10:25, *f. 12.* 1943; Fl. Brasilica 41(9): 51, *tab. 40.* 1947. Cabrera, Fl. Prov. B. Aires 4:321, *f. 98.* 1965.

E. arechavaletae H. Lév., Bull. Geogr. Bot. 21:149. 1911. TYPE: Uruguay, April–May 1911, *J. Arechavaleta*. No authentic material has been seen. H. Lév., Cat. Pl. Yun-nan.. *f. 66.* 1916.

E. sarmentaceum sensu Back. & Bakh., Fl. Java 1:262. 1963, non Hausskn., Oesterr. Bot. Z. 29: 149. 1879.

E. cinereum sensu Raven, Blumea 15:273. 1976, non A. Rich., Essai Fl. N. Z. 330. 1832.

Vigorous, perennial herbs, (10–)20–70(–110) cm tall, reproducing vegetatively by elongate leafy shoots from near the base. Stems erect, simple, or branched below, sometimes sparingly branched above, terete, yellow brown or reddish,

somewhat woody with conspicuous exfoliating epidermis at the base, villous throughout, with fine erect hairs 0.25–0.6 mm long, with an admixture of erect glandular hairs 0.1–0.2 mm long. Leaves alternate, only opposite at the first 2 or 3 nodes, thin, bright green, narrowly lanceolate to lanceolate, 1–4.7(–5.6) cm long, 0.2–0.8(–1.3) cm wide, acuminate, rarely the lower acute at the apex, regularly and remotely serrate, with 3–10(–15) forward projecting, slightly hooked teeth, 0.25–1 mm long, on each side, acute to rounded, occasionally clasping at the base, sessile, the adaxial and abaxial surfaces villous and glandular, glabrate with age, then pubescence restricted to the midrib, veins, and margin, the lateral veins inconspicuous, 2–5 on each side of the midrib, sessile. Inflorescence erect, simple. Flowers erect. Ovaries usually densely villous with erect to slightly appressed hairs and erect glandular hairs, 1–2.3 cm long, on pedicels 0–4(–9) mm long. Floral tube 0.4–0.9 mm deep, 1.1–1.6 mm across, externally villous with spreading to appressed hairs and erect glandular hairs, internally with a ring of erect villous hairs, 0.2–0.3 mm long, near the base. Sepals lanceolate, acuminate, 2.5–5 mm long, 0.9–1.2 mm wide, slightly keeled, villous with spreading to appressed and erect glandular hairs. Petals white, obovate, 2.9–4.7 mm long, 1.5–2.8 mm wide, the notch 0.5–0.8 mm deep. Anthers cream, 0.6–0.8 mm long, 0.4–0.6 mm wide; filaments cream, those of the longer stamens 1.2–2.4(–3) mm long, those of the shorter 0.8–1.4 mm long; both sets of anthers shedding directly on the stigma at anthesis and often before the flower opens. Style white, 1.4–2.5 mm long; stigma white, clavate, 0.8–2.3 mm long, 0.4–0.8 mm thick. Capsules erect, villous with spreading to slightly appressed hairs and erect glandular hairs, 2.8–6 cm long, 1.2–1.6 mm thick, on pedicels (0.4–)0.8–2.1 cm long. Seeds brown, papillose, obovoid, 0.8–1 mm long, 0.2–0.4 mm thick, the micropylar end rounded; coma white or slightly yellowish, 4–8 mm long, readily detaching. Gametic chromosome number, $n = 18$.

Distribution (Fig. 11): In Australasia, widely distributed in southeastern Australia, Tasmania, and North Island in New Zealand, rare and scattered on South Island, New Zealand; also in Java and the Lesser Sunda Islands. In South America, found most frequently in marshes and other wet, often disturbed places; in the mountainous parts of its range, most often on moist stream banks and seeps; scattered widely from eastern Santa Catarina and Rio Grande do Sul, Brazil, southward through eastern Uruguay to southern Corrientes, Entre Rios, and Buenos Aires provinces, Argentina, reaching its southern limit in the Sierra de La Ventana (38°S), also in the Sierras Grande and Chica de Córdoba. In the coastal and southern parts of its South American distribution, ranging from near sea level to approximately 200 m, occurring at much greater elevations in the Sierra Grande de Córdoba, 1,300–1,700 m, and the mountains of Santa Catarina and Rio Grande do Sul, 800–1,900 m. Flowering October to February throughout, but not until December in the Sierra Grande de Córdoba.

Representative specimens examined: ARGENTINA, BUENOS AIRES: Chacabuco, 34°38′S, 60°29′W, *without collector in 1923* (LP); Punta Lara, 34°49′S, 57°59′W, *Cabrera 1243* (LP); *Sparre 316* (S); Toloso, 34°53′S, 57°58′W, *Cabrera 7381* (F); Conchitas, 34°47′S, 58°10′W, *Castellanos in 1919* (BA); Tandil, *Castex-Jussen in 1928* (BA); Rosas, 35°58′S, 58°56′W, *Daguerre 194* (BA, MO, RSA); Curramalán, 37°28′S, 62°06′W, *Hauman in 1924* (BAA); Quilmes, 34°44′S, 58°16′W, *Hicken in 1902* (BAF); Delta del Paraná, Arroyo Guazú, *Hicken 1105* (BAF, SI), *Lanfranol 459* (SI), *Scala 114* (LP, NY); Ituzaingó, 34°40′S, 58°40′W, *Holmberg 120* (SI); Partido Tigre, Las Conchas, *Hunziker 2422* (CORD, LP, SI); Las Palmas, 34°05′S, 59°10′W, *Hunziker 7264* (CORD); Partido Pilar, Río Luján, El Cazador,

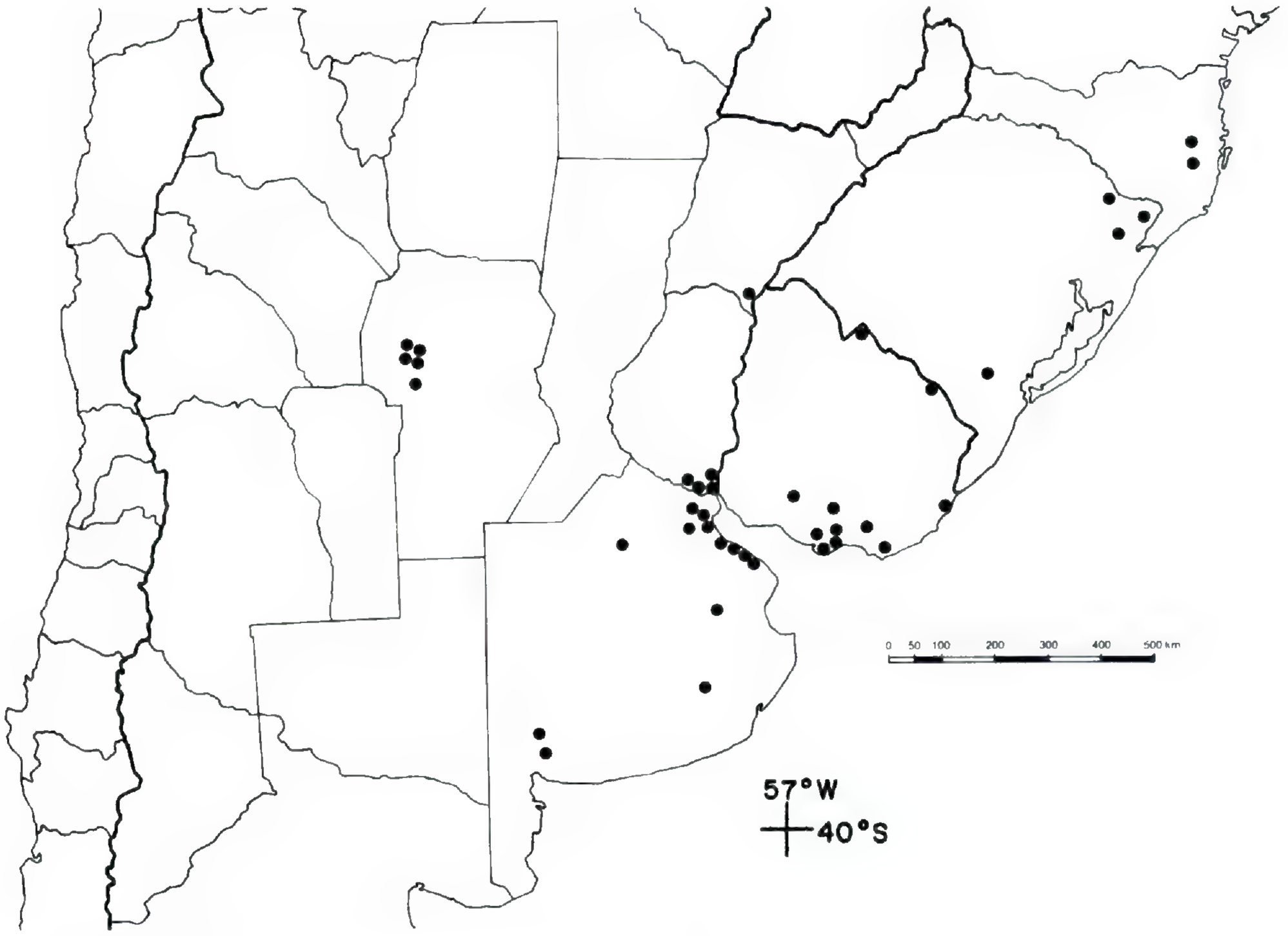


FIGURE 11. Distribution of *Epilobium hirtigerum*.

34°25′S, 58°50′W, *Mazzucconi 713* (BAB); Campana, *Parodi in 1928* (BAA, GH); San Isidro, *Parodi 10260* (BAA); Villa Elisa, *Pérez-Moreau in 1947* (BA, MO, RSA); Delta del Paraná, Mini, *Burkart 4031* (BAA, MO), *Scala 305* (LP, NY); Río Carabelas, 34°15′S, 58°43′W, *Scala in 1925* (NY); Sierra de la Ventana, *Spegazzini in 1895* (LP); La Plata, Isla Santiago, *Spegazzini in 1903* (BAB). CÓRDOBA: Valle de Los Reartes, 31°55′S, 64°34′W, *Castellanos in 1919* (UC); Sierra Achala, cuesta de la Sala Grande, *Hieronymus 856* (GOET); Dpto. Punilla, Sierra Grande, cerca del Río Yuspe, detrás del Cerro Blanco, 1,650 m, *Hunziker 10253* (CORD, MO; mixed with *E. ciliatum*); Dpto. Calamuchita, Río San Miguel, camino a Yacanto, *Krapovickas & Cristóbal 14675* (C, CTES); Dpto. Punilla, Sierra Chica, Tanticuchi, *Kurtz 4427* (CORD, DS, G, JE, LP, RSA); Sierra Grande, 3 km above Copina, 1,600 m, 31°50′S, 64°10′W, *Solomon 4131* (MO); La Cumbrecita, 1,450 m, 31°55′S, 64°15′W, *Solomon 4212* (MO); Sierra Achala, Despeñaderos, Olmedo, *Stuckert 10542* (CORD, G), *Stuckert 10813* (CORD); Dpto. Punilla, Villa García, *Stuckert 20435* (CORD), *20589* (CORD); Dpto. Cruz del Eje, Sierra de Achala, Pampa de San Luis, *Stuckert 20842* (CORD). CORRIENTES: Dpto. Monte Caseros, Estancia La Potota, *Nicora 5111* (BAA, CTES, MO). ENTRE RIOS: Delta del Paraná a Arroyo Martínez, *Boelcke 989* (BAA, MO); Ibicuy, *Burkart 3595* (BAA); Pasaje Talavera, 33°53′S, 58°55′W, *Gamero 1033* (LP); 5 km de Brazo Largo, camino a Gualeguaychú, 33°47′S, 58°36′W, *Gamero 1347* (LP); Delta del Paraná, Río Seibo, *Burkart 5122* (BAA, MO), *Cabrera 1945* (LP, NY), *Hunziker 4617* (BAB, MO); Dpto. Gualeguaychú, camino a Pt. Yerua, desvio a Nueva Escocia, *Troncoso et al. 2462* (SI).

BRAZIL, Without locality, *Sello 3186* (JE). RIO GRANDE DO SUL: Without locality, *Gaudichaud 3186* (P); Serra dos Tapes, *Lindman 913* (S, UPS); Bom Jesus, 28°42′S, 50°24′W, *Rambo 8571* (SP); San Francisco de Paula, Vila Oliva, 800 m, 29°14′S, 50°53′W, *Rambo in 1946* (B, S); Prov. Vacaria, Río das Antas, 28°30′S, 50°56′W, *Rambo in 1950* (BR, HBR, MO). SANTA CATARINA: Campos dos Padres, 1,900 m, *Reitz 2608* (HBR, MO, US); Mun. Bom Retiro, between Fazenda Santo Antonio and falls of Río Canoas, Campos dos Padres, 1,400 m, *Smith & Klein 7833* (B, HBR, MO, NY, RSA, US); Mun. Bom Jardím, Serra Geral, Campo da Serra de Oratorio, 28°22′S, 49°20′W, *Ule 1464* (CORD, P).

URUGUAY, CANELONES: Dist. Pando, *Herter 1147d* (MO, S); Barra del Arroyo Carrasco, *Legrand 864* (POM); *865* (POM), *1327* (F), *Munz 15443* (BH, GH, NY, POM), *Rosengurtt B429* (POM, US); La Floresta, *Osten 21665* (BAA, BAF, BREM, GH, MO); Arroyo Canelon Chico, *Rosengurtt 715*

(RSA). CERRO LARGO: Río Negro y Arroyo Acegua, *Rosengurtt 853* (RSA). FLORES: Maciel, Paso de Los Membrillos, *Osten 4307* (G). FLORIDA: Estancia Rincón de Santa Elena, cerca del Arroyo Timote, 33°29′S, 56°03′W, *Krapovickas 4825* (LIL). Estancia Rincón de Santa Elena, Arroyo Mansavillagia, *Rosengurtt 5808* (BR, MO, S, WTU). MALDONADO: Piriapolis, 34°54′S, 55°17′W, *Osten 5704* (CORD, SI). MONTEVIDEO: Montevideo, *Fruchard 336* (P), *Giberly 336* (K), *Gibert* (LP). ROCHA: Palmares de Costillos, 25 km N of Costillos, *Bartlett 21384* (MICH). SAN JOSÉ: Barra Santa Lucia, *Herter 1147* (F, G, GH, GOET, M, MO, NY, POM, SI, UC, US, Z), *Osten 4515* (G), *del Puerto 803* (F); Arroyo San José, 34°10′S, 55°50′W, *Herter 1147c* (Z). The following additional collections of *Epilobium hirtigerum* from Uruguay are cited in Munz (1943). Although these specimens have not been examined, their assignment to *E. hirtigerum* is nearly certain, since that is the only species known to occur in Uruguay. Munz does not indicate the Uruguayan herbaria in which the specimens are deposited, but they are most likely MVFA or MVM. CANELONES: Canelones, *Arechavaleta in 1897*; Canelón Grande, *Berro 2318*; Bañados del Arroyo Carrasco, *Berro 8791*; Carrasco, *Legrand 1043*. CAVALLEJA: Minas, Cerro Penitente, 34°20′S, 55°07′W, *Berro 5451*. RIVERA: Curticeiras, 31°04′S, 55°29′W, *Berro 4853*. SAN JOSÉ: Barra de Santa Lucía, *Chebataroff 910, Osten 4575*.

Epilobium hirtigerum can be easily recognized by its fine erect, villous and glandular pubescence, erect white flowers, elongate leafy basal shoots, and mostly alternate coarsely serrate leaves, the teeth relatively large and somewhat forward projecting. These distinctive features make *E. hirtigerum* unlike any other species. *Epilobium ciliatum* is the only other similar species in South America with white flowers.

The first collections of *E. hirtigerum* from the New World were obtained by P. Commerson in 1767 from the vicinity of Montevideo, Uruguay. As has often been the case with early collections of *Epilobium* from outside Europe, they were compared with familiar European species, and, in this case, included under the name of *E. tetragonum*. The inclusion of this distinctive taxon in *E. tetragonum* persisted until the early years of this century, although Haussknecht described the South American populations as a separate species, *E. brasiliense*, in 1879 (Haussknecht, 1879). Most subsequent workers have considered *E. brasiliense* a distinct, endemic species (Samuelsson, 1923, 1930; Munz, 1943, 1947). Only with intensive study of the Australasian species (Raven & Raven, 1976), did it become apparent that *E. brasiliense* is conspecific with the widespread and variable *E. hirtigerum*. (Reference should be made to Raven & Raven (1976) for a detailed discussion of the morphological variation in this species within Australasia.)

All South American populations are characterized by small, white, highly autogamous flowers, as are most populations in Australasia. Functional cleistogamy is very common, since the anthers often shed their pollen directly on the stigma before the flowers open. The most conspicuous variation is in the size and shape of the leaves and the pubescence of the inflorescence and ovaries. The broadest and longest leaves often occur on rather lax, weak-stemmed plants and are probably shade forms, while the smallest-leaved plants are from more open, perhaps drier sites. The majority of populations have dense, erect or slightly appressed pubescence, which gives the inflorescence and ovaries a grayish appearance. A few populations are less densely villous, but all have an abundance of erect glandular hairs.

Epilobium hirtigerum is the only species that occurs in eastern South America, with most of its range in northeastern Argentina, Uruguay, and southern Brazil. Only in the Sierra Grande de Córdoba does it grow sympatrically with any other *Epilobium* species, in this case *E. ciliatum* and *E. denticulatum*. Often all three species grow intermixed along stream banks. Occasional apparent hy-

brids with *E. ciliatum* are known (Pampa de San Luis, *Stuckert 20842,* CORD; and Arroyo del Medio, *Hieronymus 750,* CORD; pollen stainability 28% and 26%, respectively), and are particularly significant since they show that, despite the often cleistogamous flowers, *E. hirtigerum* does hybridize with other species.

12. Epilobium conjungens Skottsberg, Wiss. Ergebnisse Schwed. Südpolar-Exp. 4(4):24, *tab. 1, f. 3a–d.* 1906. TYPE: Argentina, Terr. Tierra del Fuego, Ushuaia, Martial Mountains, 810 m, 11 March 1902, *C. Skottsberg 206* (S, lectotype here designated, photograph MO; BA, S, SI, UP, isolectotypes). Samuelsson, Svensk Bot. Tidskr. 17:393. 1923.

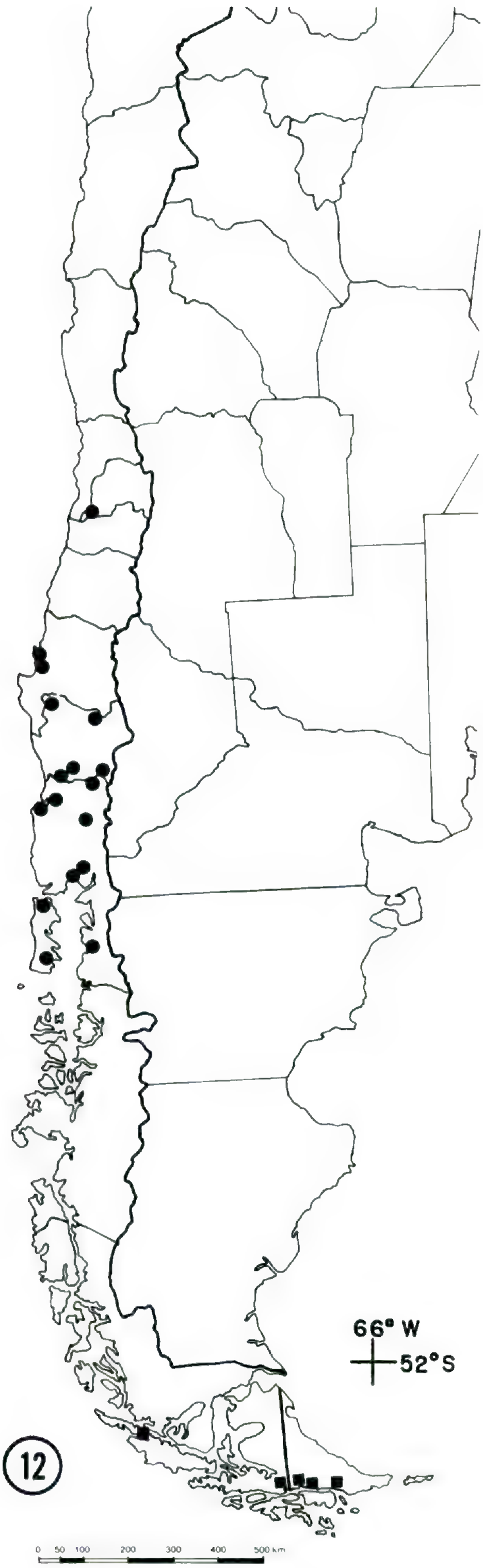
Matted, creeping, perennial herb; stems terete, prostrate, yellowish or pale brown, minutely puberulent, with hairs 0.02–0.08 mm long at the nodes, or glabrous, occasionally in descending lines from the petiole bases, internodes shorter than leaves, giving the plant a congested appearance; the stems continuing to grow and root at the nodes beyond the point where the flowers are produced. Leaves opposite, thick, dull green or sometimes reddish lustrous above, broadly elliptic to rotund or orbicular, 2.5–8.7 mm long, 1.7–6.4 mm wide, broadly obtuse to rounded, occasionally somewhat acute at the apex, entire or with 1–3(–5) obscure teeth on each side, the margin slightly revolute, obtuse, rounded, or occasionally truncate at the base, glabrous, the lateral veins obscure, none or 1, occasionally 2, on each side of the midrib, on winged petioles 1–2.3 mm long, 0.7–1.5 mm wide, merging more or less abruptly with the blade. Flowers erect, solitary and scattered in the middle and upper portions of the stem. Ovaries often reddish, glabrous, 4–6.5 mm long, on pedicels 2.5–5 mm long. Floral tube 0.4–0.7 mm deep, 1.2–2 mm across, externally and internally glabrous. Sepals lanceolate, 3.2–4 mm long, 0.9–1.2 mm wide, glabrous. Petals white to slightly pinkish, obovate, 2.8–4.4 mm long, 2.3–2.8 mm wide, the notch ca. 0.7 mm deep. Anthers cream, 0.36–0.5 mm long, 0.3–0.5 mm wide; filaments cream, those of the longer stamens 0.8–1.2 mm long, those of the shorter 0.6–0.8 mm long; both sets of stamens shedding directly on the stigma at anthesis. Style cream, 1–1.3 mm long; stigma cream, capitate, flat-topped, 0.35–0.6 mm long, 0.4–0.5 mm thick. Capsules erect, glabrous, 1.3–3.5 cm long, 0.9–1.2 mm thick, on pedicels 1–2.2 cm long. Seeds light brown, minutely papillose, narrowly obovoid, 0.7–1.1 mm long, 0.25–0.4 mm thick; coma white to slightly yellowish, 4–6 mm long.

Distribution (Fig. 12): In moist moss mats and other damp places above timberline. Known only from the southernmost mountain ranges of Tierra del Fuego facing the Beagle Channel, and Isla Desolación, at elevations of 400 to 1,000 m. Flowering January to early March.

Specimens examined: ARGENTINA, TIERRA DEL FUEGO: Estancia Harberton, Flat Top Mtn., *Goodall 1135* (MICH, NA, UC), *Moore 1391* (BAB, MO); Mountains behind Punta Segunda, E of Mt. Trapezio, *Goodall 1482* (MICH, MU, NA); Ushuaia, Monte Martial, *Goodall 4763* (BAB, MO); Sierra Sorondo, 1,000 m, 54°47′S, 67°58′W, *Moore 1978* (MO); Sierra Sorondo, above Las Cotorras, 750 m, *Santesson 462* (GB).

CHILE, XII REGIÓN (MAGALLANES): *Antártica Chilena,* Cordón Pirámide, valley E of Yendegaia airfield, 500 m, *Goodall 3822* (BAB, HIP, LTR, MICH, MO, MU, NA, SI, UC). *Magallanes,* Isla Desolación, Puerto Angosto, 400 m, 53°12′S, 73°22′W, *Dusén 684* (UPS).

This distinctive South American species is rarely seen or collected due to the inaccessibility of its habitat and very limited geographical range. The creeping



FIGURES 12–13. Distribution of *Epilobium* species.—12. *E. obscurum* (dots); *E. conjungens* (squares).—13. *E. tetragonum* (dots); *E. paniculatum* (triangles).

habit, with the stem produced beyond the flowers and rooting at the nodes, and the suppression of the typical, more or less discrete inflorescence of other species, make it unique among South American species.

From data in Raven & Raven (1976), *Epilobium conjungens* seems most closely related to *E. brunnescens,* a widespread species composed of three subspecies, two throughout New Zealand, and the third endemic in southeastern Australia (West & Raven, 1977). It differs significantly from any of these, however, in being nearly glabrous, with minute hairs only at the junction of the fused petiole bases, rarely with descending lines of scattered hairs, erect flowers with short glabrous pedicels (<5 mm) at anthesis, short fruiting pedicels (<2.2 cm), and the leaves always longer than the internodes.

All of the collections of *Epilobium conjungens* are quite homogeneous. The greatest variation is exhibited by the amount of pubescence and the size and shape of the leaves. *Epilobium conjungens* may grow sympatrically with *E. australe,* as this is the only species that reaches elevations above 400 m within the geographic range of *E. conjungens,* but they are probably separated by habitat preference.

13. Epilobium obscurum Schreb., Spicil. Fl. Lips. 147, 155. 1771. TYPE: Germany, vicinity of Leipzig. Apparently lost. (Synonymy not given.) Raven, Fl. Europ. 2:310. 1968.

Robust perennial herbs, 40–90 cm tall, reproducing vegetatively and overwintering by elongate leafy shoots produced at or near the base. Stems erect or ascendent, terete or quadrangular, freely branched above and below, becoming reddish purple with age, strigillose with hairs 0.15–0.25 mm long, densely so in the inflorescence, glabrate below and then pubescence restricted to raised descending lines from the decurrent petiole bases. Leaves mostly opposite, alternate above, thin, dull blue green, narrowly lanceolate to lanceolate, or lance-elliptic, 2.5–5 cm long, 0.5–1 cm wide, acute or acuminate at the apex, more or less regularly denticulate with 10–30 teeth on each side, obtuse, or occasionally acute at the base, strigillose on the margins, abaxial midrib, and veins, glabrous adaxially, the lateral veins prominent, impressed above, 4–6 on each side of the midrib, sessile. Inflorescence erect, sparingly branched, the leaves subtending the flowers much reduced in size. Flowers erect. Ovaries often reddish, strigillose, usually densely so, occasionally with erect glandular hairs 0.1–0.15 mm long, 1.5–2.5 cm long, on pedicels 0.6–1.3 cm long. Floral tube occasionally reddish, 0.6–1.2 mm deep, 1.4–2.3 mm across, externally strigillose with a few erect glandular hairs, internally with a ring of erect villous hairs, 0.2–0.3 mm long, near the base. Sepals lanceolate, 2–3.4 mm long, 0.8–1.5 mm wide, slightly keeled at the base, strigillose. Petals rose purple, obovate, 4–5.5(–6.8) mm long, 2–3.2(–4.4) mm wide, the notch 0.8–1.4 mm deep. Anthers cream or yellowish, 0.4–0.9 mm long, 0.4–0.9 mm wide; filaments cream, those of the longer stamens 1.2–2.2 mm long, those of the shorter 0.8–1.3 mm long, the longer stamens, and occasionally the shorter, shedding pollen directly on the stigma at anthesis. Capsules erect, strigillose, 3–6 cm long, 1–1.4 mm thick, on pedicels 0.4–1.5(–2) cm long. Seeds brown, papillose, obovoid, 0.7–0.9 mm long, 0.3–0.4 mm thick; coma white, 4–8 mm long, readily detaching. Gametic chromosome number, $n = 18$.

Distribution (Fig. 12): Throughout Europe, except for much of the European USSR, and the northernmost parts; also in the Azores, Madeira, Canary Islands, locally in Morocco, and the Amanus Mountains of Turkey. Introduced and widely naturalized in New Zealand, and perhaps only recently established in Tasmania (Raven & Raven, 1976). In South America, introduced and widely naturalized in central Chile from Aculeo (Maipo Prov.) to Isla Chiloé, at elevations from near sea level to 1,200 m. Frequent and weedy along roadside ditches, but also occurring in rocky or sandy stream beds, seeps, or other moist, disturbed situations. Flowering November to March.

Specimens examined: CHILE, REGIÓN METROPOLITANA (SANTIAGO): *Maipo,* Aculeo, 33°53′S, 70°53′W, *Bertero 236* (P). VIII REGIÓN (BÍO-BÍO): *Concepción,* 5 km SE of Concepción, 20 m, 36°50′S, 73°05′W, *Solomon 4414* (MO); San Pedro, *Suwalsky in 1954* (CONC). XI REGIÓN (ARAUCANÍA): *Cautín,* 2 km E of Villarrica, 200 m, 39°17′S, 72°12′W, *Solomon 4521* (MO); Termas de Palguín, 700 m, 39°21′S, 71°45′W, *Solomon 4526* (MO). *Malleco,* 5 km below Vegas Blancas, 600 m, 37°45′S, 72°58′W, *Solomon 4460* (MO); 3 km below Vegas Blancas, 950 m, 37°45′S, 72°58′W, *Solomon 4471* (MO); Termas de Tolguaca, 1160 m, 38°15′S, 71°45′W, *Solomon 4482* (MO). X REGIÓN (LOS LAGOS): *Chiloé,* Lago San Miguel, 43°04′S, 73°40′W, *Marticorena et al. 106* (CONC); Ancud, 41°52′S, 73°50′W, *Seki 103* (CONC). *Llanquihue,* 20 km E of Puerto Varas, 50 m, 41°15′S, 72°47′W, *Solomon 4597* (MO); 5 km E of Puerto Montt, *Wall & Sparre in 1947* (S). *Palena,* Chaitén, *Marticorena 1693* (CONC). *Valdivia,* La Paz, 39°24′S, 73°44′W, *Eaton in 1976* (MO); Teja Island, 39°50′S, 73°20′W, *Ramírez in 1975* (MO), *Romero in 1966* (VALD); *Sautos in 1959* (VALD), *Westermeier in 1973* (VALD); Río Cau-cau, *Schlegel 6882* (VALD); 1 km W of Coñaripe, 220 m, 39°34′S, 72°00′W, *Solomon 4540* (MO); Lago Santo Domingo, 8 km SE of Valdivia, 10 m, 39°50′S, 73°10′W, *Solomon 4558* (MO); Corral, 10 m, 39°50′S, 73°26′W, *Solomon 4571* (MO); Fundo San Martín, *Woerner in 1953* (CONC, mixed with *E. puberulum*).

This distinctive, primarily European, species can now be found over a large part of central Chile. It is most easily distinguished by the erect glandular hairs that are restricted to the floral tube, the elongate leafy basal shoots, the narrowly lanceolate to elliptic, denticulate leaves, and the rose-purple petals. Commonly it grows in roadside ditches, intermixed with *Epilobium ciliatum,* the species with which it is most likely to be confused. *Epilobium ciliatum,* however, is distinctive in having ridged seeds with a chalazal appendage, leafy basal rosettes or turions, glandular hairs present throughout the inflorescence, and white or pale pink petals. In New Zealand there has been great confusion between *E. ciliatum* and *E. obscurum*. Petrie, in fact, described a new native species, *E. erectum,* based on a mixed collection of these two species (Raven & Raven, 1976). Only rarely was *E. obscurum* observed growing sympatrically with *E. glaucum* (Near Coñaripe, Lago Calafquén, Prov. Valdivia) or *E. puberulum* (Fundo San Martín, Prov. Valdivia), both of which are sometimes weedy.

Epilobium obscurum was first collected in Chile at Aculeo (Prov. Maipo) in March 1828 (*Bertero 236,* P). The next collections were not made until 1947 (*Wall & Sparre,* S) at Puerto Montt. Apparently no one has previously recognized this species or recorded it from South America. Steudel did base *E. hispidulum* (nomen nudum) on Bertero's collection, but this name passed rapidly into oblivion (Steudel, 1840).

All of the available collections of *Epilobium obscurum* are relatively uniform in habit, leaf shape, pubescence, etc., the only exception being a specimen with unusually large flowers (petals 6.8 mm long) from Puerto Montt (*Wall & Sparre in 1947*).

The frequency of *E. obscurum* in the field today, and the lack of any collec-

tions during the latter part of the nineteenth or early twentieth century when a great deal of botanical work was being conducted in central Chile, leads one to surmise that *E. obscurum* may have been introduced more than once, and that any nineteenth century introductions did not persist, or did so only marginally. In fact, *E. obscurum* has not been re-collected in the vicinity of Aculeo since Bertero's time, thus making the northernmost known locality for a recent collection from near Concepción (*Suwalsky in 1954,* CONC-18972), about 350 km farther south. It is certainly possible that heavy disturbance of the forest regions, and extensive road construction during the past 30 years have allowed the rapid dispersal of *E. obscurum* into areas that were formerly relatively remote, accounting for its apparent explosive spread in recent years.

A probable hybrid between *Epilobium obscurum* and *E. ciliatum* was collected 2.8 km below Vegas Blancas, near Parque Nacional Nahuelbuta (Prov. Malleco, *Solomon 4471,* MO), where both species were common in and around a swampy pasture. Its hybrid nature is indicated by the presence of erect glandular hairs throughout the inflorescence, the broader, more strongly toothed leaves, the presence of what appear to be turion scales at the base of the plant, poor capsule development, and low seed set. The pollen fertility of this specimen is 26%, a figure that is characteristic of crosses between species with the BB and AA chromosomal arrangement.

14. Epilobium tetragonum subsp. **lamyi** (F. Schultz) Nyman, Consp. Flor. Eur. 247. 1879. *E. lamyi* F. Schultz, Flora 27:806. 1844. TYPE: France, "Solo argilloso in arvis humidis prope Limoges," *P. Lamy*. Type material not seen. (Complete synonymy not given.) Samuelsson, Svensk Bot. Tidskr. 29:9. 1930. Raven, Fl. Europ. 2:30. 1968.

Clumped perennial herbs, 20–100 cm tall, overwintering and reproducing vegetatively by leafy rosettes produced at the base late in the season. Stems erect, branched above, terete or quadrangular, strigillose all around in the upper portions and usually below, or glabrate below, with raised descending lines from the decurrent petiole bases. Leaves mostly opposite, alternate in the inflorescence, thin, dark blue green, often reddish, especially below, lanceolate to oblong-lanceolate, 2.5–5 cm long, 0.5–1.5 cm wide, acute to acuminate at the apex, regularly serrulate with 5–20 teeth on each half, acute to rounded at the base, strigillose on the adaxial and abaxial midribs, veins, and margins, lateral veins prominent, 3–5 on each side of the midrib, on poorly defined petioles 0.5–2 mm long. Inflorescence erect, branched, the leaves subtending the flowers reduced in size. Flowers erect. Ovaries densely strigillose, 1.5–3 cm long, on pedicels 0.3–1.5 cm long. Floral tube 0.8–1.2 mm deep, 1–1.4 mm across, externally strigillose, internally with a ring of erect villous hairs 0.2–0.3 mm long. Sepals lanceolate, 2.5–4 mm long, 0.9–1.3 mm wide, slightly keeled, strigillose. Petals rose purple, obovate, 2.5–5 mm long, 2.1–3.5 mm wide, the notch 1–1.6 mm deep. Anthers yellow, 0.6–1.1 mm long, 0.4–0.6 mm wide; filaments rose purple, those of the longer stamens 1.4–2.5 mm long, those of the shorter 0.7–1.4 mm long, the longer stamens, and occasionally the shorter, shedding pollen directly on the stigma at anthesis. Style white or slightly purplish at the base, 1.5–3 mm long; stigma white,

clavate, 1.4–2 mm long, 0.6–1.1 mm thick. Capsules erect, strigillose, 5–9 cm long, 1–1.6 mm thick, on pedicels 0.5–2 cm long. Seeds brown, coarsely papillose, obovoid, 0.7–1.2 mm long, 0.35–0.5 mm thick, the micropylar end rounded; coma white, 4–7 mm long, readily detaching.

Distribution (Fig. 13): Throughout Europe, southwestern Asia, and North Africa; perhaps introduced, but now widely distributed in South Africa; introduced in New Zealand, where it is rapidly becoming naturalized, and sparingly in Australia and North America. Known as an introduction in South America only from Chile, where it is a rare, and perhaps persistent garden weed in a few cities. Flowering November to January.

Specimens examined: CHILE, REGIÓN METROPOLITANA (SANTIAGO): *Santiago*, Santiago, *Claude-Joseph 931* (US); Nuñoa, Barrio de Santiago, *Claude-Joseph 1245* (US). VIII REGIÓN (BÍO-BÍO): *Concepción*, Concepción, *Oehrens in 1978* (CONC, MO). X REGIÓN (LOS LAGOS): *Llanquihue*, Puerto Montt, *Pfister in 1942* (CONC).

Epilobium tetragonum subsp. *lamyi* has been collected only four times during the period from 1919 to 1978, twice in Santiago, and once each in Concepción and Puerto Montt. The two collections from Santiago are so similar to each other morphologically that they may have been derived from the same source, although they were collected two years apart. This entity is certainly rare in South America. Its widely scattered occurrence as a garden or street weed in cities might be the result of several introductions, perhaps by contaminated garden seeds from Europe, or some other unknown European source.

The specimens from Chile have all been retained in *Epilobium tetragonum* subsp. *lamyi*, based on the short-petiolate upper leaves and the usually oblong-lanceolate to lanceolate leaf shape (Raven, 1968; Clapham et al., 1962). There is considerable question as to whether or not *E. tetragonum* subsp. *lamyi* should be considered taxonomically distinct from *E. tetragonum* subsp. *tetragonum* (Raven, pers. comm.). Only additional, more detailed studies of this variable species in its native area will be able to resolve this problem.

Epilobium tetragonum subsp. *lamyi* can be distinguished from *E. obscurum* by its leafy basal rosettes, serrulate leaves, and lack of glandular pubescence on the floral tube, and from *E. ciliatum* by its papillose seeds, rose purple flowers, and lack of glandular hairs.

15. Epilobium paniculatum Nutt. ex Torr. & Gray, Fl. N. Amer. 1:490. 1840. nom. conserv. prop. TYPE: Oregon, "Rocky Mountains and the Columbia plains," 1834–35, *T. Nuttall* (NY, lectotype; BM, GH 2 sheets, PH, isolectotypes; W. Jepson, Fl. Calif. 2:571. 1936). (Complete synonymy not given.) Munz, N. Amer. Fl. II. 5:207. 1965.

E. brachycarpum Presl, Reliquiae Haenkeanae 2:30. 1831, non Leight., Ann. Nat. Hist. 8:401. 1841; nec sensu Munz, Aliso 4:489. 1960; N. Amer. Fl. II. 5:219. 1965. Nom. prop. rejic., Hoch & Raven (1981a). TYPE: "Mexico," most likely California, Monterey Co., Monterey, 13–23 September 1791, *T. Haenke* (PR, holotype). This is the only locality within the known distribution of *E. paniculatum* where the Malaspina Expedition stopped.

The following description is based on South American plants only: Erect annual herb, 30–60 cm tall, with a long tap root. Stems branched above, terete, glabrous, often somewhat woody at the base, with conspicuously exfoliating epidermis. Leaves mostly alternate, only a few lower nodes opposite, gradually

reduced upwards, with fascicles of small leaves in the axils, often early deciduous, dull green, sometimes slightly glaucous, thick, linear to narrowly lanceolate, 1–3.5 cm long, 2–4.5 mm wide, often conduplicate, acuminate at the apex, remotely denticulate with 3–10 teeth on each side, acuminate at the base, glabrous, the lateral veins apparently absent, on poorly defined petioles 0–3 mm long. Inflorescence erect, paniculately branched, the branches thin, the leaves subtending the flowers reduced to subulate bracts, and fused to the base of the pedicel for 1 to 2 mm. Flowers erect. Ovaries with erect glandular hairs, 0.1–0.5 mm long, or glabrous, 0.9–1.6 cm long, the pedicels glandular pubescent or glabrous, 1–6 mm long. Floral tube reddish, 1.6–2.4 mm deep, 1.2–1.6 mm across, externally glandular pubescent or glabrous, internally with a ring of erect villous hairs ca. 0.1 mm long near the base. Sepals reddish, glabrous, lanceolate, 2–2.7 mm long, 0.8–1 mm wide. Petals rose purple, obovate, 3–4 mm long, 1.2–2 mm wide, the notch 0.5–1.9 mm deep. Anthers cream, 0.8–1 mm long, 0.4–0.5 mm wide; filaments cream, those of the longer stamens 1–1.2 mm long, those of the shorter 0.5–0.8 mm long, the longer stamens shedding pollen directly on the stigma at anthesis. Style cream, 1.8–2.7 mm long; stigma cream, long clavate to capitate, 0.4–1.2 mm long, 0.4–0.5 mm thick. Capsules erect, glandular pubescent or glabrous, 1.9–3.2 cm long, 1.3–1.7 mm thick, on pedicels 3–9 mm long. Seeds mottled gray brown, finely papillose, broadly obovoid, 1.4–1.6 mm long, 0.7–0.8 mm thick, with a conspicuous constriction of the micropylar end 0.3–0.45 mm long; coma white to yellowish brown, 5–7 mm long, readily detaching. Gametic chromosome number, $n = 12$.

Distribution (Fig. 13): Throughout much of western North America from British Columbia to Saskatchewan, North and South Dakota, south to Arizona and New Mexico. Introduced in Argentina, from southwestern Neuquén, south to northwestern Chubut. Open, dry, often disturbed ground. Flowering January to February.

Specimens examined: ARGENTINA, CHUBUT: Between El Bolsón and Leleque, *Zöllner 7646* (MO, NA). NEUQUÉN: Dpto. Aluminé, Aluminé, *Crespo & Giangualani 2006* (BAB, MO); Dpto. Los Lagos, Valle Encantado, Rio Limay, 40°44′S, 71°07′W, *Crespo et al. 2306* (BAB, MO).

The introduced *Epilobium paniculatum* is the only member of the monotypic section *Xerolobium* of western North America. It is easily distinguished from all other South American species by its often conduplicate, early deciduous, glabrous, alternate leaves, the relatively large seeds with a conspicuous micropylar constriction, simple tap root, and annual habit.

The three known South American populations are quite uniform in morphology and habit. They all have simple, clavate or capitate stigmas and small flowers, a widespread feature in North American populations, although other North American populations are characterized by 4-lobed stigmas and much larger flowers (Raven et al., 1981). The most striking morphological variation is in the presence or absence of erect glandular hairs. Plants may be either glabrous, and with hairs only on the pedicels, ovaries, and floral tube. Glabrous or pubescent individuals can be found in the same population (*Zöllner 7646*), so the absence of hairs may be under a simple genetic control.

This distinctive addition to the introduced flora of Argentina was first collected in 1974 between El Bolsón and Leleque, Chubut Prov. (*Zöllner 7646*), and reported by Seavey & Raven (1977c). Since then, it has been collected twice,

increasing its range northward to Aluminé, Neuquén Prov., a distance of 300 km. Undoubtedly this species will continue to expand its range in the semi-arid and montane habitats of western Patagonia.

EXCLUDED NAMES

Epilobium lineare Larrañaga, Escritos de D. A. Larrañaga 1:25. 1922 (Publ. Inst. Hist. Geog. Uruguay), non Muhlenberg, Cat. 39. 1813. The plants are described as having yellowish flowers and linear leaves. Yellow or cream flowers are unknown in *Epilobium*, except for *E. luteum*, a North American species. This species is probably a member of the Cruciferae.

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INDEX

Synonyms are italicized. Page numbers of main entries are in boldface.

Arracacia 257
Boisduvalia 238
Chamerion (Raf.) Raf. 263
Chamaenerion Séquier 238, 263
Cordylophorum (Nutt. ex Torr. & Gray) Rydb. 263
  suffruticosum (Nutt.) Rydb. 263
Crossostigma Spach. 263
  lindleyi 263
Epilobieae 237
Epilobium
  Sect. Chamaenerion 238, 239
  Sect. *Cordylophorum* Nutt. ex Torr. & Gray 238, 263
  Sect. Crossostigma 238
  Sect. Epilobium 238–239, 243–244, 248, 258
  Sect. Xerolobium 238–239, 264, 328
  Sect. Zauschneria 238
  Subgen. *Chamerion* Raf. 263
  aconcaguinum R. Phil. 288
  adenocaulon 295
  aequinoctiale Samuelsson 268
  albiflorum R. Phil. 288
  alpestre (Jacq.) Korck. 244
  alpinum 262, 300
  alsinifolium Vill. 244
  amenum Raf. 263

anagallidifolium Lam. 244, 297
andicolum Hausskn. 267, 275–276
andinum R. Phil. 300, 309
angustifolium L. 238–239
antarcticum (Hook. f.) Kuntze 308
arechavaletae H. Lév. 318
argentinum Samuelsson 289
asplundii Samuelsson 268, 275
assurgens Samuelsson 268
australe Poeppig & Hausskn. 239–241, 243–245, 248–249, 251, 253, 257–262, 265, 294, 299–301, 303, 305, **307–314**, 318, 324
  var. *andinum* (R. Phil.) Samuelsson 309
  var. *lechleri* (R. Phil. & Huasskn. ex Hausskn.) Samuelsson 308
  var. *pumilum* Samuelsson 309, 314
barbeyanum H. Lév. 240, 244–245, 248–249, 251, 253, 257–259, 261, 263, 265, 284, 299, **302–305**, 318
bolivianum Samuelsson 268, 274, 276
bonplandianum H.B.K. 262, 267, 274, 288
brachycarpum Presl 327
brasiliense Hausskn. 253, 318, 321
brunnescens 324
caesiovirens Samuelsson 289
caesium Hausskn. 262, 267, 274, 280, 288
canum (Greene) Raven 238
chilense Hausskn. 252, 262, 288, 294–295
  var. *latifolium* Samuelsson 288
  var. *macrum* Samuelsson 289
  var. *valdiviense* (Hausskn.) Hoss. 288
ciliatum Raf. 239–245, 248–249, 251–252, 256–262, 265–266, 273–274, 277, 280, 287–**288–299**, 302, 305, 309, 311, 313–314, 318, 321–322, 325–326
  subsp. ciliatum 244–245, 249, 252, 294–296, 300, 309
  subsp. glandulosum 243
  subsp. watsonii 245, 247, 249, 280
cinereum 318
clavatum 244
conjungens Skottsberg 239–242, 248, 251, 253–254, 256, 258–259, 262, 264, 302, **322–324**
constrictum Samuelsson 289
cunninghamii Hausskn. 288
deflexum Samuelsson 309, 313
deminutum Samuelsson 268
densifolium 239–243, 245, 248–249, 251, 257–261, 265, 301, 304–**305–308**, 314, 318
denticulatum Ruiz & Pavón 241–245, 248–249, 251–252, 257–262, 265, **267–277**, 280–281, 283–284, 286–287, 299, 303, 307, 321
  var. *aberans* Samuelsson 268, 275
  var. *confertum* Samuelsson 268
  var. *macropetalum* Samuelsson 268
duriaei Gay ex Godron 245
ecomosum 296
erectum Petrie 325
fragile Samuelsson 239–240, 243, 248, 251, 259, 264, 266, 273–274, 277, **281–283**
franciscanum Barbey 280
glaberrimum Barbey 247, 252
glandulosum 288, 295
glaucum R. Phil. 239–240, 243–245, 247–249, 251, 253, 257–261, 265, 277, 280, 299–302, 308, 311, **314–318**
  var. *stenophyllum* Macloskie & Dusén 315
gracile R. Phil. 284
haenkeanum Hausskn. 260, 277, 280
helodes H. Lév. 267
hirsutum 263
hirtigerum A. Cunn. 238, 241–245, 247–248, 251, 253, 256, 258–259, 261, 265, 277, 279, 287, 299, **318–322**
hirtum Samuelsson 241, 243, 260, 268, 274, 276
hispidulum 325
holosericeum 296
hookerianum Hausskn. ex Skottsberg 288
hornemannii Reichenb. 244
interruptum Samuelsson 309
junceum Forst. f. ex Spreng. 267, 318
  var. *hirtigerum* (A. Cunn.) Curtis 318
latifolium L. 238
lechleri var. *antarcticum* Macloskie 308, 313
leiphyton Samuelsson 289, 297
lignosum R. Phil. 305
lineare Larrañaga 329
littorale 313
longipes Samuelsson 289
lutem Pursch 244
magellanicum R. Phil. & Huasskn. ex Huasskn. 252, 288, 296
meridense Hausskn. 267, 274
  var. *condensatum* Samuelsson 268
  var. helodes 275
mexicanum 315
microphyllum A. Rich 247
nivale Meyen 239–240, 243–245, 248–249, 251, 253, 257, 259–262, 265, 281, 283, 285, **299–302**, 309, 317
nubigenum R. Phil. 315
nummulariifolium A. Cunn. 253
obcordatum A. Gray 244
obscurum Schreb. 238, 244–245, 248, 260, 266, 294, 299, 323, 324–325, 327
oreganum 243, 295
palustre 247
paniculatum Nutt. ex Torr. & Gray 238–239, 264–265, 279, 301, 323, **327–329**
patagonicum Rendle 315
pauciflorum R. Phil. 243, 305, 307
pedicellare Presl 241–242, 244, 248, 251, 259–262, 266–267, 273–274, 276–**277–281**, 288, 315
  β latifolium Walp. 288
pedunculare A. Cunn. 253
  pedunculatum R. Phil. 284
  peruvianum Hausskn. 278, 280
  platystigmatosum 245
  puberulum Hook. & Arn. 240, 242–245, 247–248, 251–252, 256, 259–261, 267, 274, **283–288**, 299, 325
  ramosum R. Phil. 315
  repens 274
  rigidum Hausskn. 238
  santa-cruzense Dusén 288, 297
  sarmentaceum 318
  saximontanum 297
  tetragonum L. 262, 266, 288, 313, 318, 321, 323
    β antarcticum Hook. 262, 308, 313
    subsp. lamyi 238, 326–327
    subsp. tetragonum 327
  transandinum Samuelsson 309
  valdiviense Hausskn. 252, 288, 294
    var. *alboffi* Macloskie 288
  watsonii 295
Gunnera tinctoria (Mol.) Mirbel 258
Hypericum 256
Isoetes savatieri Franch. 258
Lleracia 257
Nothofagus 255, 257, 302
  pumilio 302
Perezia bellidifolia (Phil.) Reiche 258
  megalantha Speg. 258
  multiflora 257
Pyrogennema Lunell 263
  angustifolium (L.) Lunell 263
Stephanomeria 297
  exigua Nutt. 297
Zauschneria Presl 238, 263
  californica Presl 263

A REVISION OF THE SOUTHWESTERN SPECIES OF *AMSONIA* (APOCYNACEAE)[1]

STEVEN P. MCLAUGHLIN[2]

ABSTRACT

Taxonomic studies based on herbarium and field plot observations were conducted on all species of *Amsonia* (Apocynaceae) native to the southwestern United States and northwestern Mexico. Within subgenus *Sphinctosiphon*, data obtained in this study from recent collections support the retention of *A. jonesii*, *A. kearneyana*, *A. palmeri*, *A. peeblesii*, and *A. tharpii*. *Amsonia hirtella* and its varieties are reduced to synonymy with *A. palmeri*. In subgenus *Longiflora*, which is here elevated from its previous status as a section of subgenus *Sphinctosiphon*, *A. grandiflora* and *A. longiflora* are retained, and *A. salpignantha* is treated as a variety of *A. longiflora*. In subgenus *Articularia*, one species with two varieties is recognized: *Amsonia tomentosa* var. *tomentosa*, including *A. brevifolia*; and *A. tomentosa* var. *stenophylla*, including *A. arenaria* and *A. eastwoodiana*. A key to the species and taxonomic synopsis are included.

Amsonia was described by Thomas Walter in 1788 and was first monographed and later revised by Woodson (1928, 1938). The taxonomic history of the genus was thoroughly reviewed by Woodson (1928) and will not be repeated here. The two studies by Woodson differed substantially in their treatments of the southwestern species, which he later (1948, p. 238) characterized as being "ambiguous species." Many of these southwestern species were known from only a few specimens. However, during the past 40 years numerous additional collections have been made of all species from the Southwest; therefore, it now seems appropriate to reexamine this particular complex group.

Amsonia species are herbaceous perennials from a woody, long-lived root. The leaves are simple, alternate to subverticillate, the middle and lower ones typically broadest, those above increasingly narrow distally. The flowers are white to light blue or pink, gamopetalous, with five calyx lobes, corolla lobes, and stamens. The distinct, unappendaged anthers are included within the tube of the salverform corolla. The pistil is composed of two distinct ovaries joined by a common style. The fruit is a pair of multiseeded follicles. The seeds are corky and lack an aril or coma. The distinct, unappendaged anthers place *Amsonia* in the tribe Plumeroideae of the Apocynaceae. The most closely related genus is *Haplophyton* A.DC., which differs principally from *Amsonia* in having comose seeds.

As treated here, the southwestern species constitute three distinct subgenera. *Amsonia* subgenus *Articularia* Woodson has articulate-moniliform follicles while those of subgenera *Sphinctosiphon* (K. Schumann) Woodson and *Longiflora* (Woodson) McLaughlin are continuous (Fig. 1). The corollas in subgenus *Sphinc-*

[1] Janice E. Bowers and Steven D. Sutherland assisted in the field collections, including considerable work on their own time. Paul Mirocha provided the graphics, and Ann Rosenthal and Debra Zavala typed the several drafts of the manuscript. Dr. Charles T. Mason, Jr., arranged for loans of herbarium material and provided valuable critical review of the manuscript. Their help is gratefully acknowledged.

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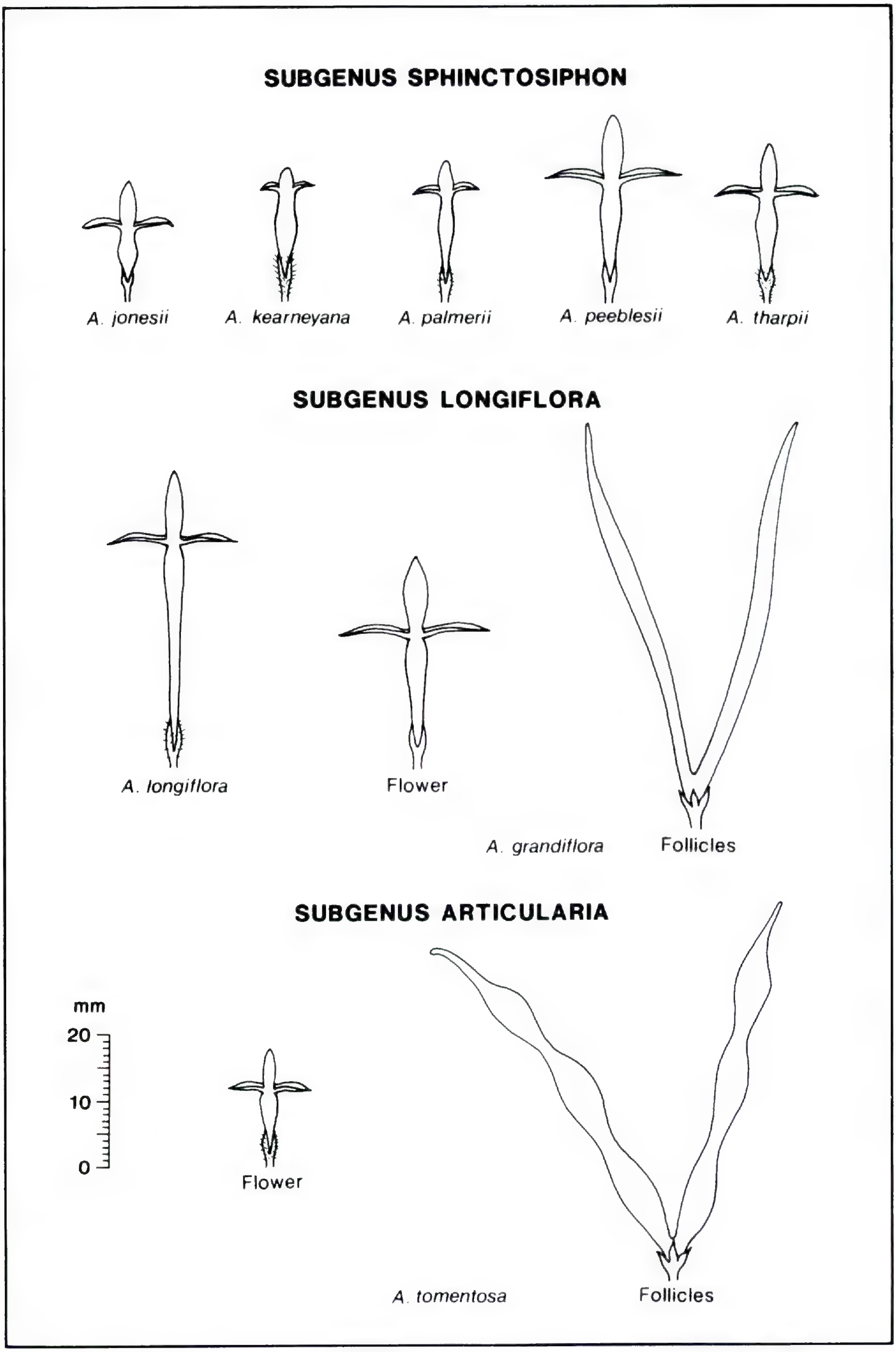

FIGURE 1. Corolla and follicle shape in southwestern *Amsonia* spp. Follicle morphology in subgenus *Sphinctosiphon* spp. is similar to that illustrated for *A. grandiflora* in subgenus *Longiflora*.

tosiphon have relatively short tubes that are only moderately constricted at the apex while those of subgenus *Longiflora* have longer, slender tubes that are markedly constricted at the apex (Fig. 1). The corolla tubes in subgenus *Articularia* are short with the apex markedly constricted.

The remainder of the species of *Amsonia* are all placed in subgenus *Amsonia*, which consists of eight species native to the southeastern United States and one species from Japan. I have not collected or worked with this last subgenus. The species of subgenus *Amsonia* are known from many collections and appear to be much better defined than the southwestern species, as shown by the similarity in the two treatments of the former by Woodson (1928, 1938).

METHODS

Collections were examined of all southwestern *Amsonia* species from ARIZ, ASU, MNA, MO, and TEX. Additional material of selected taxa from RSA, CAS, and NY were examined. Measurements of characters traditionally used to define and separate species were made on 300 specimens, over two-thirds of which have been collected since the last revision (Woodson, 1938). Characters measured include width of broadest stem leaves, corolla tube and lobe length, and seed length and width. Plants of four taxa of subgenus *Articularia* were grown in the greenhouse and in a field plot for additional observations and measurements (Table 3).

SUBGENUS *SPHINCTOSIPHON* (K. SCHUMANN) WOODSON

Twelve taxa have been described in this section, seven of which are currently recognized in either the Arizona (Kearney & Peebles, 1960) or Texas (Correll & Johnston, 1970) floras (Table 1). Species and varieties have been distinguished principally on the basis of pubescence, length of the corolla tube and lobes, and leaf shape (Woodson, 1928, 1938; Kearney & Peebles, 1960; Correll & Johnston, 1970). *Amsonia jonesii* Woodson, *A. peeblesii* Woodson, and *A. tharpii* Woodson are fairly distinct species, but treatments of *A. hirtella* Standl., *A. hirtella* var. *pogonosepala* (Woodson) Wiggins, *A. kearneyana* Woodson, and *A. palmeri* Gray vary considerably. Woodson (1928) accepted all four, along with *A. standleyi* Woodson, as distinct species; but he later revised the group recognizing only *A. palmeri* and *A. hirtella* (Woodson, 1938).

Gray (1877) described the first species in subgenus *Sphinctosiphon*, *A. palmeri*, from specimens grown from seed collected by Palmer in Arizona, exact location unknown. These plants were glabrous with narrow leaves and short corolla lobes. Plants meeting Gray's description occur only in Yavapai County, Arizona. Plants described as *A. kearneyana* (Woodson, 1928) have similar flowers, but the plants are pubescent and have considerably broader leaves. Woodson (1938) combined the two taxa and expanded the description of *A. palmeri* to include the variation in both forms. Kearney & Peebles (1960) followed Woodson (1928) in narrowly defining *A. palmeri* while Correll & Johnston (1970) followed the broader interpretation in Woodson (1938), with the result that most specimens from west Texas referable to *A. palmeri* using the Texas manual would be identified as *A. hirtella* using Arizona Flora.

TABLE 1. Range of variation of diagnostic characters of traditionally accepted taxa of *Amsonia* from the Southwest. 1. Based on Woodson (1928); 2. Based on Woodson (1938).

Taxon	Pubescence		Leaf Width (mm)	Corolla		Seeds	
	Foliage	Calyx		Tube Length (mm)	Lobe Length (mm)	Length (mm)	Width (mm)
Subgenus *Sphinctosiphon*							
A. hirtella var. *hirtella*							
Kearney & Peebles (1960) interpretation[1]	+	+	7–14	11–16	4–7	6–9	1.5–2.5
Correll & Johnston (1970) interpretation[2]	+	+	~10	10–17	5–7	?	?
A. hirtella var. *pogonosepala*	–	+	8–18	10–16	3–7	6–8	1.0–2.5
A. jonesii	–	–	14–30	6–10	4–8	8–11	2.0–2.5
A. kearneyana	+	+	11–17	12–15	2–4	8–11	3.0–4.0
A. palmeri							
Kearney & Peebles (1960) interpretation[1]	–	– (+)	5–9	11–14	2–5	6–8	1.0–2.0
Correll & Johnston (1970) interpretation[2]	+ (–)	+ (–)	4–8	8–12	3–5	6–9	1.5–2.5
A. peeblesii	–	–	4–9	15–19	5–12	8–11	1.5–2.5
A. tharpii	+	+	9–12	13–15	6–9	7–9	2.0–3.0
Subgenus *Longiflora*							
A. grandiflora	–	–	3–6	16–19	10–15	8–11	2.0–3.0
A. longiflora	–	–	1–4	23–40	7–17	5–8	1.5–2.5
A. salpignantha	+	+	2–5	31–45	7–13	5–8	1.5–2.5
Subgenus *Articularia*							
A. arenaria	+	+	3–6	8–11	5–9	14–21	3.5–5.0
A. brevifolia	–	–	8–25	7–12	3–8	9–19	3.0–5.0
A. eastwoodiana	–	–	5–13	7–12	4–7	9–15	3.0–5.0
A. tomentosa	+	+	9–22	7–12	4–9	8–15	3.0–5.0
A. tomentosa var. *stenophylla*	+	+	3–9 (16)	9–12	4–7	11–19	3.5–6.0

Woodson (1928) believed that seeds of *A. kearneyana* were sterile. This observation, coupled with the similarity in flower morphology and geographic distributions, as known at the time, probably accounts for his later inclusion of *A. kearneyana* within *A. palmeri*. I have observed 66% germination of seeds collected from the type (and only known) locality of *A. kearneyana*. I have made other observations that may explain Woodson's belief that *A. kearneyana* does not produce viable seed. Both *A. grandiflora* Alexander and *A. kearneyana* occur in southern Arizona within the range of the stinkbug, *Chlorochroa ligata*. Following the wet winter of 1978–1979, this insect was abundant on *A. grandiflora*, attacking the seed and destroying the embryo. Seed collected in 1979 was hollow and showed 0% germination. The winter of 1979–1980 was drier and few stinkbugs were observed. *Amsonia grandiflora* seed collected in 1980 from the same population showed nearly 100% germination. It is probable that the seeds of *A. kearneyana* available to Woodson had been exposed to this insect.

Amsonia kearneyana has shorter (2–4 mm) corolla lobes and larger (3–4 mm

TABLE 2. Geographic variation within *Amsonia palmeri* (sensu lato). Measurements given are means (in mm) for all members of a sample.

Region	No. Specimens Examined	% Pubescent		Leaf Width	Corolla	
		Foliage	Calyx		Tube	Lobe
Mohave-Yavapai Cos., Arizona	20	0	50	7.5	12.5	3.5
Maricopa-Pinal-Graham Cos., Arizona	22	32	100	12.5	13.7	4.5
Cochise Co., Arizona and Hidalgo Co., New Mexico	11	64	100	9.3	13.5	4.4
Southwest Texas	14	93	93	6.0	9.9	4.5

broad) seeds than most other collections of *Amsonia* from the Southwest (Table 1). All specimens from Arizona referable to *A. hirtella* var. *hirtella* that have relatively short (~4 mm) corolla lobes also have narrower leaves, effectively differentiating them from *A. kearneyana*. The only collections that I have seen that approach *A. kearneyana* in seed size are those of Stephen White from northeastern Sonora at ARIZ (see synopsis, below), which have seeds 2.5–3.5 mm broad. Corolla lobes in these Sonoran plants are somewhat longer (4–5 mm) than those of *A. kearneyana*.

Amsonia palmeri has been separated from *A. hirtella* on the basis of corolla lobe length and ratio of length of lobe to length of tube. Woodson (1938) characterized *A. palmeri* as having corolla lobes 3–5 mm long, about one-fourth the length of the tube, and *A. hirtella* as having corolla lobes 5–7 mm long, about one-half the length of the tube. However, all specimens referable to either taxon from Arizona to west Texas overlap broadly in these corolla characters (Table 1).

No set of characters consistently separate specimens referred to *A. palmeri*, *A. hirtella* var. *hirtella*, and *A. hirtella* var. *pogonosepala*. All collections of these taxa appear to me to represent one widespread, variable species (Table 2). Pubescence is of particularly questionable diagnostic value. Plants from the northwest part of the range are glabrous except for the calyx, and populations of *A. palmeri* sensu Gray from Yavapai County, Arizona occasionally have ciliate calyx lobes. Both plants with glabrous and plants with pubescent foliage occur in the same populations throughout the central part of the range and in northeastern Sonora (Fig. 2). Pubescent plants are most common in west Texas. Leaves are narrowest at the northwest and southeast ends of the range. Corolla tubes are shortest in west Texas and the lobes are shortest in plants from northwest Arizona. The variation in these traits is more or less continuous and I find no reasonable basis for segregating varieties on the basis of these characters.

Subgenus *Sphinctosiphon*, in summary, consists of one widespread species, *A. palmeri*, and four more restricted species: *A. jonesii*, *A. kearneyana*, *A. peeblesii*, and *A. tharpii* (Fig. 2), which have larger seeds, on average, than *A. palmeri* (Table 1). Specimens of *A. palmeri* may be either pubescent or glabrous, often within the same population, but *A. jonesii* and *A. peeblesii* are always glabrous while *A. kearneyana* and *A. tharpii* are always pubescent.

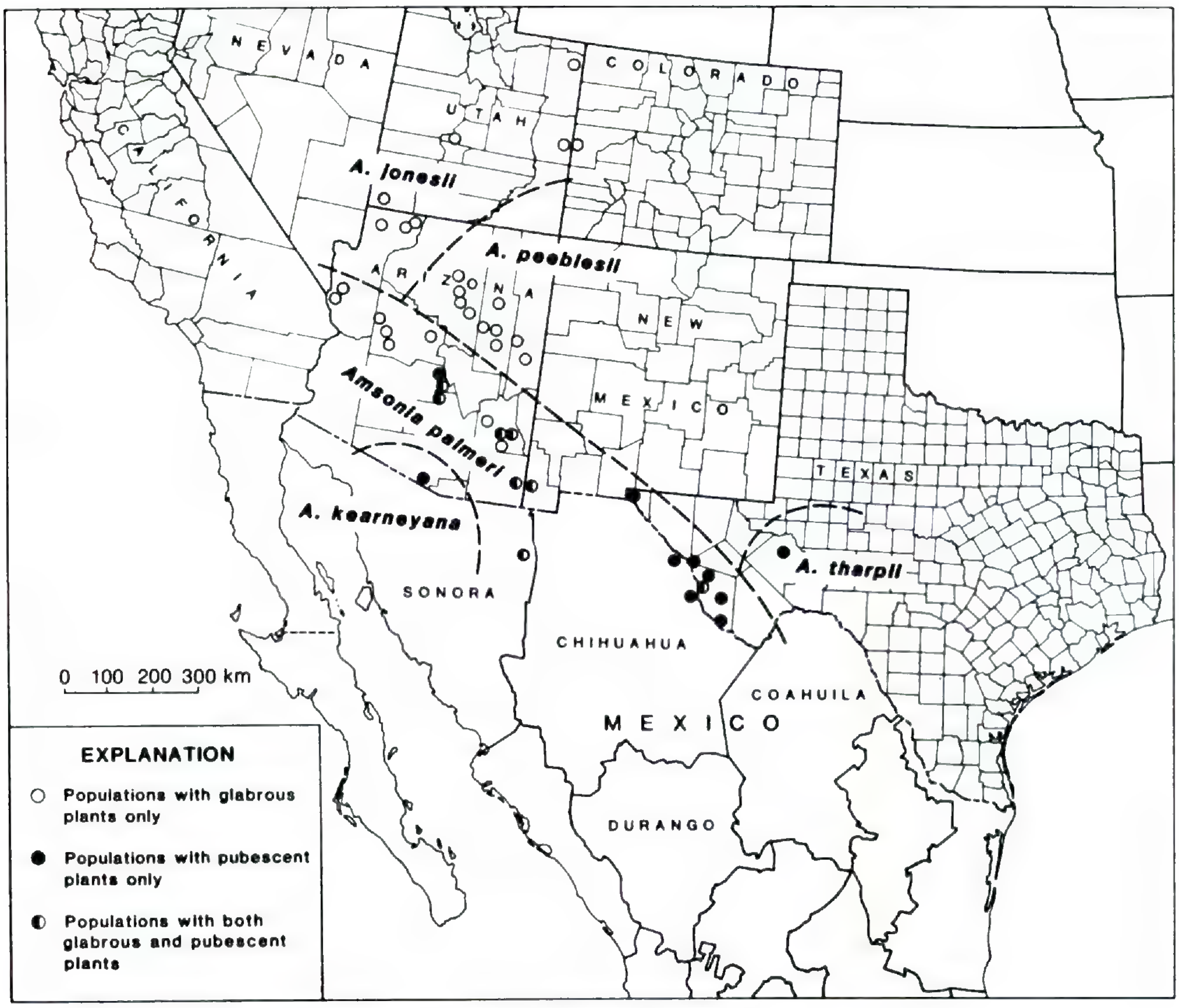

FIGURE 2. Distribution of *Amsonia* subgenus *Sphinctosiphon* taxa.

SUBGENUS *LONGIFLORA* (WOODSON) McLAUGHLIN

Woodson (1928, 1938) recognized three species in this taxon, which he treated as a section within subgenus *Sphinctosiphon*. *Amsonia grandiflora* Alexander from southern Arizona and northwestern Mexico has shorter corolla tubes, larger seeds, and broader leaves than either *A. longiflora* Torr. or *A. salpignantha* Woodson (Table 1). Woodson separated the latter two species on the basis of pubescence, corolla lobe length, and geographic range. He characterized *A. longiflora* as glabrous with corolla lobes 11–13 mm long, occurring in extreme west Texas; and *A. salpignantha* as pubescent with corolla lobes 5–8 mm long, occurring from the Trans-Pecos region to the eastern end of the Edwards Plateau.

Amsonia grandiflora is a reasonably distinct species, but recent collections from Texas, New Mexico, and Coahuila show a broader overlap between pubescent and glabrous plants than was previously known. Pubescent plants are now known from west Texas and New Mexico and both forms occur in Tule Canyon of the Rio Grande River between Brewster County, Texas, and Coahuila, but populations with both glabrous and pubescent plants have not been recorded (Fig.

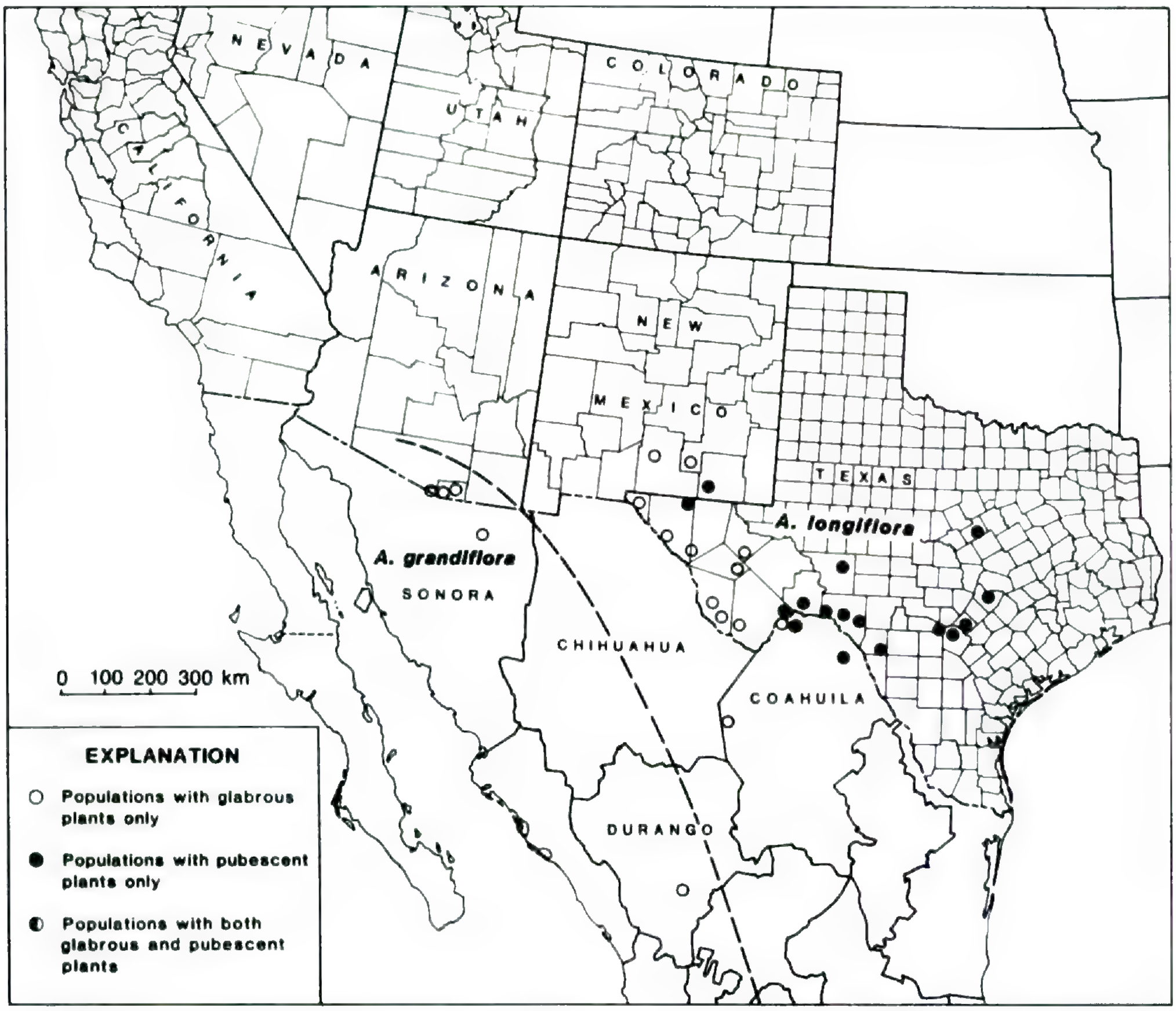

FIGURE 3. Distribution of *Amsonia* subgenus *Longiflora* taxa. Solid circles are localities for *A. longiflora* var. *salpignantha*, open circles east of dashed line are localities for *A. longiflora* var. *longiflora*.

3). Among pubescent specimens there is considerable variation in the density and distribution of trichomes. Pubescent and glabrous plants overlap broadly in corolla lobe length, corolla tube length, leaf width, and seed size (Table 1).

Amsonia longiflora and *A. salpignantha* do not appear to me to be sufficiently distinct to warrant recognition as two species. However, glabrous and pubescent plants do exhibit much greater geographic segregation than either the *A. palmeri* complex discussed above or the subgenus *Articularia* plants discussed below. Therefore it does seem reasonable to recognize varieties, a largely western, glabrous *A. longiflora* var. *longiflora* and a largely eastern, pubescent var. *salpignantha*. Further exploration of the Rio Grande Valley and Trans-Pecos regions could possibly result in the discovery of populations containing both forms.

SUBGENUS *ARTICULARIA* WOODSON

The five taxa that have traditionally comprised this group are *A. brevifolia* Gray and *A. tomentosa* Torr. & Frém. from the Mohave Desert of California, Nevada, and Western Arizona; *A. eastwoodiana* Rydb. and *A. tomentosa* var.

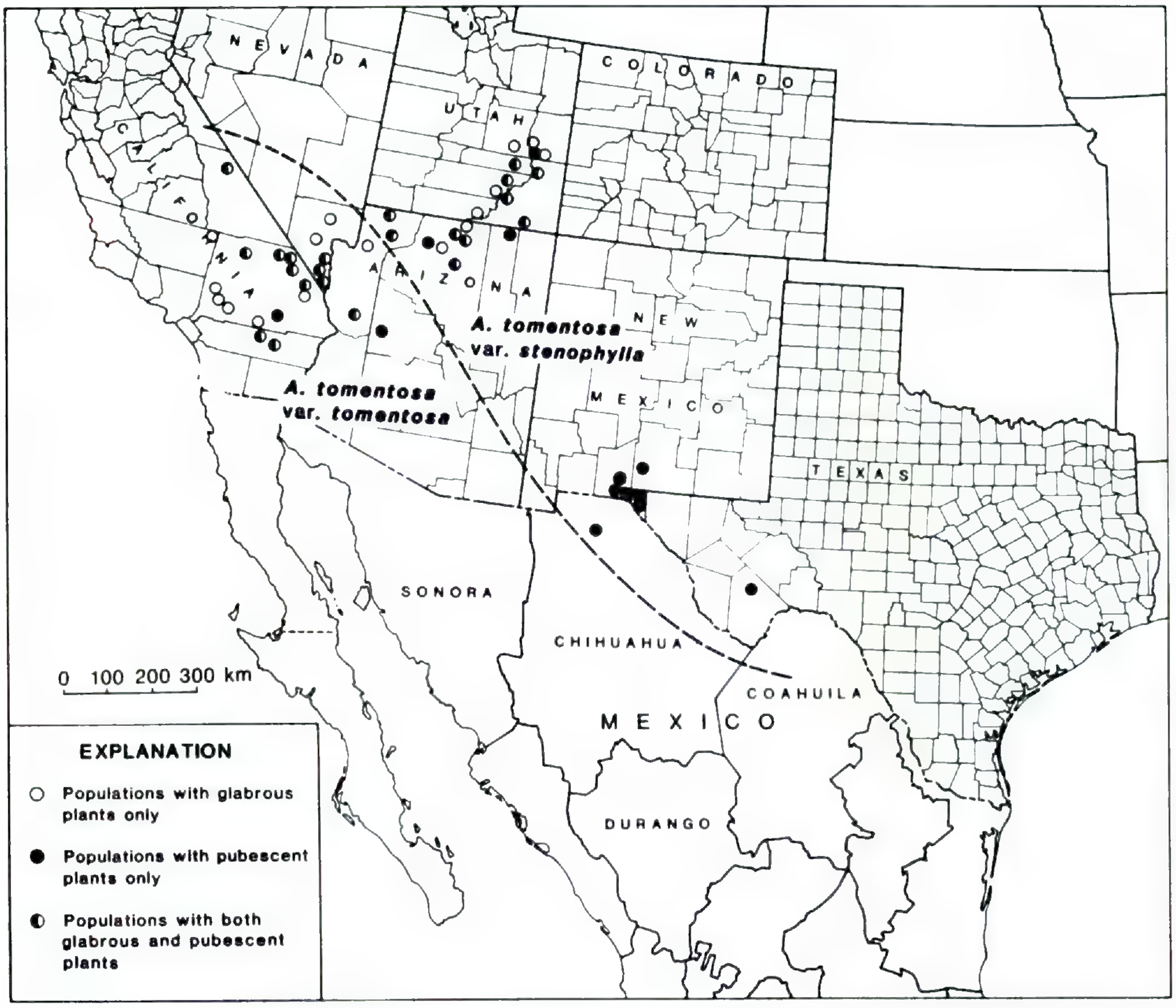

FIGURE 4. Distribution of *Amsonia* subgenus *Articularia* taxa.

stenophylla Kearney and Peebles from northern Arizona and Utah; and *A. arenaria* Standl. from New Mexico, west Texas, and Chihuahua. Pubescence, leaf shape, corolla tube length, and seed size have been used as distinguishing characters.

Specimens from the Mohave Desert typically have broad, ovate leaves. Glabrous (*A. brevifolia*) and tomentose (*A. tomentosa*) forms are usually found growing together (Fig. 4). Woodson (1928) noted that seeds of *A. brevifolia* were noticeably smaller than those of *A. tomentosa*, but I have found seed size to be highly variable in all subgenus *Articularia* taxa (Table 1). *Amsonia eastwoodiana* and *A. tomentosa* var. *stenophylla* are narrower-leaved counterparts of the Mohave Desert plants, the former glabrous and the latter tomentulose. The two forms also occur in mixed populations in both northern Arizona and Utah.

The two glabrous species, *A. brevifolia* and *A. eastwoodiana*, have been separated on the basis of leaf shape and corolla tube length. Woodson (1928, 1938) gave corolla tube ranges of 7–10 mm for *A. brevifolia* and 9–17 mm for *A. eastwoodiana*, but I have found ranges of 7–12 mm for both (Table 1). The original description of *A. eastwoodiana* was based on two disparate elements, a plant with fruit from Utah and one with flowers from Arizona (Rydberg, 1913). The

former specimen is an *A. eastwoodiana* as known today, but the latter is clearly *A. peeblesii*. I have encountered numerous specimens of *A. peeblesii* without fruit misidentified as *A. eastwoodiana* because of the incorrect dimensions given for corolla tube length in the keys of Woodson (1928, 1938) and Kearney & Peebles (1960). The corollas of *A. eastwoodiana* and *A. peeblesii* are actually quite different in shape and size but those of *A. brevifolia* and *A. eastwoodiana* are virtually indistinguishable.

Kearney & Peebles (1939) described the pubescent, narrow-leaved plants of northern Arizona and Utah as *A. tomentosa* var. *stenophylla*. Many specimens of this variety are not distinguishable from *A. arenaria* specimens from west Texas and New Mexico. It is notable that only tomentulose plants occur in the latter areas (Fig. 4).

Leaf shape in subgenus *Articularia* does show definite geographic trends although exceptions do occur. *Amsonia brevifolia* and *A. tomentosa* have typically ovate leaves 15–25 mm broad, but a few specimens collected in San Bernardino and Riverside Counties, California, and Clark County, Nevada, have lanceolate leaves 8–11 mm broad. Likewise, *A. eastwoodiana* and *A. tomentosa* var. *stenophylla* have typically oblong-lanceolate blades 3–10 mm broad. At Cameron in Coconino County, Arizona, I found one *A. tomentosa* var. *stenophylla* plant with leaves 16 mm broad in a population with leaves otherwise consistently less than 5 mm broad. In the Grand Canyon, a natural corridor connecting the ranges of *A. brevifolia* and *A. eastwoodiana*, plants with lanceolate leaves 11–15 mm broad are common.

I grew plants from seeds of *A. brevifolia*, *A. tomentosa*, *A. eastwoodiana*, and *A. tomentosa* var. *stenophylla* in the greenhouse and in a field plot at Tucson. Survival of seedlings in the greenhouse was poor. Data from surviving plants in the field plot are presented in Table 3. Progeny of three of the parent seed sources segregated into both pubescent and glabrous forms. In collection no. 2194 of *A. brevifolia*, no pubescent plants were produced in the field but 4 of 55 greenhouse seedlings developed pubescence. Although none of the offspring of *A. tomentosa* var. *stenophylla* in the field plot were glabrous, 4 of 8 greenhouse seedlings of another lot were glabrous. Seedlings of all plants in both the greenhouse and field plot were glabrous initially—pubescence typically was not expressed until the fourth or fifth leaf was produced. None of the plants have flowered. Leaf shape in the offspring resembled that of the parent plants. Seeds from *A. eastwoodiana* and *A. tomentosa* var. *stenophylla* produced plants with significantly longer and narrower leaves than plants grown from seed of *A. brevifolia* and *A. tomentosa*.

I have found no consistent set of characters to support the traditional segregation of species in subgenus *Articularia*. From west to east across the range of the subgenus, there are several trends in morphology: toward the east pubescent plants are more common, leaves are narrower, and flowers and seeds are slightly larger. Similar trends were noted in both subgenera *Sphinctosiphon* and *Longiflora*. I interpret the entire *Articularia* complex as one variable species. Field plot observations of progeny do support the recognition of two generally distinguishable varieties, an ovate-leaved *A. tomentosa* var. *tomentosa* in the west and a lanceolate to linear-leaved var. *stenophylla* in the east.

TABLE 3. Pubescence and leaf dimensions of plants of *Amsonia* subgenus *Articularia* grown in experimental plots, Tucson, Arizona. Collection numbers are those of the author. Means within a column not followed by same letter are significantly different ($p < .05$).

Parent Plants				Offspring				
Traditional Identification	Collection No.	Pubescence	Leaf-Shape	Total Number	Number Pubescent	Mean Leaf Length (mm)	Mean Leaf Width (mm)	L:W ratio
						Means		
A. brevifolia	2194	No	ovate	18	0	41.3 a	15.9 a	2.7 a
A. brevifolia	2492	No	ovate	20	4	37.1 a	13.6 a	2.8 a
A. tomentosa	2491	Yes	ovate	16	11	39.8 a	14.0 a	2.9 a
A. eastwoodiana	2208	No	linear-lanceolate	7	2	59.4 b	7.2 b	8.3 b
A. tomentosa var. *stenophylla*	2507, 2509	Yes	linear-lanceolate	5	5	51.0 b	7.1 b	7.6 b

KEY TO THE SOUTHWESTERN SUBGENERA, SPECIES, AND VARIETIES OF *AMSONIA*

1a. Follicles markedly constricted between seeds; corolla tube short, 7–12 mm long, distinctly constricted at the apex. Subgenus *Articularia*.
  2a. Leaves ovate, (8–)10–25 mm broad; plants of California, Nevada, and western Arizona. ---------- 8a. *A. tomentosa* var. *tomentosa*
  2b. Leaves oblong-lanceolate to linear-lanceolate, 3–13(–16) mm broad; plants of northern Arizona, Utah, New Mexico, Texas, and Chihuahua. ---------- 8b. *A. tomentosa* var. *stenophylla*

1b. Follicles not markedly constricted between seeds; corolla tube either longer, 16–45 mm, or not distinctly constricted at the apex.
  3a. Corolla tube long, 16–45 mm, distinctly constricted at apex; leaves narrow, 1–6 mm broad. Subgenus *Longiflora*.
    4a. Corolla tube 16–19 mm long; foliage glabrous; plants of Santa Cruz Co., Arizona, Sonora, and Durango. ---------- 7. *A. grandiflora*
    4b. Corolla tube 23–45 mm long; plants with either glabrous or pubescent foliage.
      5a. Foliage glabrous; plants of southern New Mexico, west Texas, Coahuila, and Chihuahua. ---------- 6a. *A. longiflora* var. *longiflora*
      5b. Foliage pubescent; plants of Southern New Mexico, west Texas to east end of Edwards Plateau, and Coahuila. ---------- 6b. *A. longiflora* var. *salpignantha*
  3b. Corolla tube shorter, 6–19 mm long, not distinctly constricted at apex; leaves 4–30 mm broad. Subgenus *Sphinctosiphon*.
    6a. Seeds broad, typically 3–4 mm in width; foliage pubescent; corolla lobes 2–4 mm long; plants of Baboquivari Mts., Pima Co., Arizona. ---------- 3. *A. kearneyana*
    6b. Seeds narrower, usually less than 2.5 mm broad; foliage either glabrous or pubescent; corolla lobes (2–)4–12 mm long.
      7a. Leaves ovate, 14–30 mm broad; foliage glabrous; plants of northwestern Arizona, Utah, and western Colorado. ---------- 2. *A. jonesii*
      7b. Leaves linear to elliptic-lanceolate, 3–15 mm broad; foliage glabrous or pubescent.
        8a. Plants low growing, generally less than 20 cm tall; leaves noticeably dimorphic, lower leaves elliptic-lanceolate, upper leaves linear; foliage hirtellous; plants of Pecos Co., Texas. ---------- 5. *A. tharpii*
        8b. Plants taller, generally more than 30 cm tall; leaves not noticeably dimorphic, instead gradually narrower distally; foliage glabrous or hirtellous.
          9a. Stem much branched below inflorescence, the latter barely surpassing the foliage; corolla tube 15–19 mm long, lobes 5–12 mm long; foliage glabrous; plants of northwestern Arizona. ---------- 4. *A. peeblesii*

9b. Stem sparingly branched below inflorescence, the latter well surpassing the foliage; corolla tube 10–15 mm long, lobes 2–7 mm long; foliage glabrous or hirtellous, often within the same population; plants widespread from Mohave Co., Arizona, southeast to Presidio Co., Texas. ---------- 1. *A. palmeri*

Amsonia subgenus **Sphinctosiphon** (K. Schumann) Woodson, Ann. Mo. Bot. Gard. 15:411. 1928. TYPE: *A. palmeri* Gray.

1. Amsonia palmeri Gray, Proc. Am. Acad. 12:64. 1877. TYPE: United States, New Mexico, without additional locality information, 1851–1852, *Wright 1669* (GH, neoholotype; MO!, neoisotype). Described from plants grown from seed, type assigned by Woodson (1928).

A. fremonti Rydb., Bull. Torrey Bot. Club 40:465. 1913. Nomen nudum.
A. hirtella Standl., Proc. Biol. Soc. Wash. 26:118. 1913. TYPE: United States, New Mexico, Grant Co., *Mearns 117* (US, holotype).
A. pogonosepala Woodson, Ann. Mo. Bot. Gard. 15:412. 1928. *A. hirtella* var. *pogonsepala* (Woodson) Wiggins, Contr. Dudley Herb. 4:21. 1950. TYPE: United States, Arizona, San Francisco Mts., *Rusby 256* (MO!, holotype; NY, PH, isotypes).
A. standleyi Woodson, Ann. Mo. Bot. Gard. 15:412. 1928. TYPE: United States, New Mexico, without additional locality information, 1851–1852, *Wright s.n.* (GH, holotype).
A. arizonica Nels., Am. J. Bot. 18:432. 1931. TYPE: United States, Arizona, Yavapai Co., 20 mi. S of Ashfork, *Nelson 10247*, (RM, holotype).
A. biformis Nels., Am. J. Bot. 32:288. 1945. TYPE: United States, Arizona, Graham Co., W of Duncan, *Nelson 11278–9* (RM, holotype).

Herbaceous perennial, glabrous or pubescent, 30–80 cm tall; lower leaves lanceolate to linear, 4–18 mm broad; upper leaves linear-lanceolate; calyx lobes subulate, glabrous, ciliate along margins, or densely pubescent, 2–7 mm long; corolla tube 8–17 mm long, broadest below the apex, moderately constricted at the orifice, lobes 2–7 mm long; follicles 2–13 cm long; seeds cylindrical, corky, 6–10 mm long, 1.0–2.5 mm broad. Mohave County, Arizona, southeastward below the Mogollon Rim in Arizona to southwest Texas, northeastern Sonora, and northern Chihuahua.

This is a variable species that is not readily separable into varieties. Pubescence cannot be used as a diagnostic character since glabrous and densely pubescent forms occur in mixed populations throughout much of the range. On an annotation to a herbarium specimen (*Peebles 11655*, ARIZ!), Woodson noted that plants grown from seed of a single follicle segregated into glabrous and pubescent forms. The materials Woodson (1928) designated as the type specimens for *A. palmeri* (*Wright 1669*) and *A. standleyi* (*Wright s.n.*), which differ primarily in pubescence, bear similar notations and probably were collected from the same population.

Pubescent specimens from the Rio de Bavispe region of northeastern Sonora (*McLaughlin & Bowers 2556*, ARIZ) are very similar to *A. kearneyana* in vegetative morphology. However, corolla lobe length (4–5 mm) in both glabrous and pubescent plants from this area exceeds that of typical *A. kearneyana* (2–4 mm long). The only fruiting specimens from this area (*White 505, 3021*, ARIZ!) have seeds 2.5–3.5 mm long, wider than typical *A. palmeri* but narrower than typical *A. kearneyana*. The presence of both glabrous and pubescent plants in the same

same population and the relatively long corolla lobes suggest to me a much closer affinity of these plants to *A. palmeri* than to *A. kearneyana*. Additional material from northeastern Sonora would be valuable.

2. **Amsonia jonesii** Woodson, Ann. Mo. Bot. Gard. 15:414. 1928. *A. latifolia* Jones, Cont. West. Bot. 12:50. 1908. Not *A. latifolia* Michx., Fl. Bor. Am. 1: 121. 1803. TYPE: United States, Utah, Sevier Co., Monroe, *M. E. Jones 6446* (RSA, holotype, MO!, isotype). RSA 75995 (*Jones,* 6 June 1913), which is labeled as a type for *A. jonesii,* is a specimen of *A. tomentosa* var. *stenophylla.*

Herbaceous perennial, glabrous, 15–50 cm tall; lower leaves ovate, 14–30 mm broad; upper leaves lanceolate, 3–10 mm broad; calyx lobes ovate to lanceolate, 1–4 mm long; corolla tube 6–10 mm long, broadest below the apex, slightly constricted at the orifice, lobes 4–8 mm long; follicles 1.5–9 cm long; seeds cylindrical, corky, 6–8 mm long, 2.0–2.5 mm broad. Northwestern Arizona, Utah, and western Colorado.

Specimens lacking fruit can be mistaken for glabrous forms of *A. tomentosa* var. *tomentosa*. The latter species occurs within or south of the Grand Canyon in Arizona, and its corolla tube is broadest at the apex and markedly constricted at the orifice. Corolla lobes of *A. tomentosa* are typically about ½–⅔ the length of the tube while those of *A. jonesii* are nearly as long as the tube.

3. **Amsonia kearneyana** Woodson, Ann. Mo. Bot. Gard. 15:415. 1928. TYPE: United States, Arizona, Pima Co., Baboquivari Mts., *Thackery 55* (MO!, holotype).

Herbaceous perennial, pubescent, 40–90 cm tall; lower leaves lanceolate, 11–17 mm broad, upper leaves linear-lanceolate, 3–8 mm broad; calyx lobes subulate, 3–6 mm long; corolla tube 12–15 mm long; broadest below the apex, slightly constricted at the orifice, lobes 2–4 mm long; follicles 3–10 cm long; seeds cylindrical, corky, 8–11 mm long, 3–4 mm broad. Baboquivari Mountains, Pima County, Arizona.

4. **Amsonia peeblesii** Woodson, Bull. Torrey Bot. Club 63:35. 1936. TYPE: United States, Arizona, Coconino Co., near Leupp, *Kearney and Peebles 9568* (MO!, holotype).

Herbaceous perennial, glabrous, 40–90 cm tall; lower leaves oblong-linear, 4–9 mm wide, upper leaves linear, 1–2 mm wide; calyx lobes ovate to linear, 2–7 mm long; corolla tube 13–19 mm long, broadest below the apex, slightly constricted at the orifice, lobes 5–10 mm long; follicles 2–10 cm long; seeds cylindrical, corky, 8–11 mm long, 1.5–2.5 mm broad. Coconino, Navajo, and Apache Counties, Arizona.

Flowering specimens of this species have often been misidentified as the glabrous form of *A. tomentosa* var. *stenophylla* (*A. eastwoodiana*). The corolla tube of the latter is shorter (7–12 mm) and markedly constricted at the apex.

5. **Amsonia tharpii** Woodson, Ann. Mo. Bot. Gard. 35:237. 1948. TYPE: United States, Texas, Pecos Co., 21 mi. NE of Ft. Stockton, *Warnock 46183* (MO!, holotype; TEX!, isotype).

Herbaceous perennial, pubescent, 10–20 cm tall; leaves distinctly dimorphic, lower leaves elliptic-lanceolate, 9–12 mm broad, upper leaves linear-lanceolate, 1–4 mm broad; calyx lobes narrowly lanceolate to subulate, 2–6 mm long; corolla tube 13–16 mm long, broadest below the apex, slightly constricted at the orifice, lobes 6–9 mm long; follicles 2–12 cm long; seeds cylindrical, corky, 7–9 mm long, 2–3 mm broad. Pecos County, Texas.

Amsonia subgenus **Longiflora** (Woodson) McLaughlin comb. nov. TYPE: *A. longiflora* Torr.

Woodson (1928) treated this taxon as a section of subgenus *Sphinctosiphon* because the follicles are continuous in both. The flowers of subgenus *Longiflora* species, however, are distinctly different from those in subgenus *Sphinctosiphon*. In subgenus *Longiflora,* the corolla lobes are long (usually >10 mm) and spreading and the corolla tubes are long (>15 mm), slender, with a distinct constriction at the apex, but in subgenus *Sphinctosiphon* the lobes are shorter (usually <10 mm), erect to spreading, and the tubes are shorter (usually <15 mm, except in *A. peeblesii*) and only moderately constricted at the apex. The anthers in subgenus *Longiflora* are positioned at the top of the corolla tube just below the constriction, but in subgenus *Sphinctosiphon* (except occasionally in *A. jonesii,* which has a very short corolla tube) the anthers are positioned lower in the tube, from about midway in *A. palmeri* and *A. peeblesii* to the upper ¼ in *A. tharpii*. In addition, the broadest leaves in subgenus *Longiflora* are very narrow (>10 times as long as broad) while those in subgenus *Sphinctosiphon* are broader (typically 2–8 times as long as broad). Subgenus *Longiflora* populations also occur in more mesic habitats than either subgenus *Sphinctosiphon* or *Articularia* populations. These differences, I believe, justify elevating *Longiflora* to subgeneric rank.

6. **Amsonia longiflora** Torr., Bot. Mex. Bound. Surv. 159. 1859. TYPE: United States, Texas, El Paso Co., near El Paso, *Wright 1168* (NY, holotype; GH, MO!, isotypes).

Herbaceous perennial, glabrous or pubescent, 20–60 cm tall; lower leaves linear-lanceolate, 1–5 mm broad, upper leaves filiform, 1 mm broad; calyx lobes linear, 2–9 mm long; corolla tube 23–45 mm long, broadest at the apex, markedly constricted at the orifice, lobes 7–17 mm long; follicles terete, 4–20 cm long; seeds cylindrical, corky, 5–8 mm long, 1.5–2.5 mm broad.

6a. Amsonia longiflora Torr. var. **longiflora.**

Plants glabrous, corolla tubes generally 25–40 mm long. Southern New Mexico, west Texas, and Coahuila.

6b. Amsonia longiflora var. **salpignatha** (Woodson) McLaughlin, comb. nov. *Amsonia salpignantha* Woodson, Ann. Mo. Bot. Gard. 15:417. 1928. TYPE:

United States, Texas, Hamilton Co., *Reverchon 1557* (F, holotype; MO! isotype).

Plants hirtellous, corolla tubes generally 35–45 mm long. Southern New Mexico, west Texas east to the Edwards Plateau, and northern Coahuila.

7. **Amsonia grandiflora** Alexander, Torreya 34:116. 1934. TYPE: United States, Arizona, Santa Cruz Co., near Patagonia, *Peebles, Harrison & Loomis 6986,* (US, holotype; ARIZ!, isotype).

Herbaceous perennial, glabrous, 40–90 cm tall; lower leaves linear-lanceolate, 3–6 mm broad; upper leaves linear, 1–3 mm broad; calyx lobes linear, 3–7 mm long; corolla tube 16–20 mm long, broadest at the apex, markedly constricted at the orifice, lobes 10–15 mm long; follicles terete, 4–15 cm long; seeds cylindrical, corky, 8–11 mm long, 2–3 mm broad. Santa Cruz County, Arizona, adjacent northeastern Sonora, and a single collection (*Palmer 90,* MO!) from Durango.

Amsonia subgenus **Articularia** Woodson, Ann. Mo. Bot. Gard. 15:418. TYPE: *A. tomentosa* Torr. & Frém.

8. **Amsonia tomentosa** Torr. & Frém., Torr. in Frém. Rep. Calif. 316. 1845. TYPE: United States, without locality information, *Fremont,* 2nd exped. (NY!, holotype).

Herbaceous perennial, glabrous or tomentose, 20–60 cm tall; lower leaves ovate to linear, 3–25 mm broad, upper leaves lanceolate to filiform, 1–10 mm broad; calyx lobes linear, 2–9 mm long; corolla tube 7–12 mm long, broadest at the apex, markedly constricted at the orifice, lobes 3–9 mm long; follicles articulate-moniliform, 2–8 cm long; seed elliptic, corky, 8–21 mm long, 3–6 mm broad.

8a. Amsonia tomentosa var. **tomentosa.**

A. brevifolia Gray, Proc. Am. Acad. 12:64. 1877. *A. brevifolia* var. *tomentosa* Jepson, Man. Fl. Pl. Calif. 768. 1925. TYPE: United States, Arizona, Mohave Co., Mokiah Pass, *Palmer 302* (GH, holotype).

A. lanata Alexander, Torreya 34:117. 1934. TYPE: United States, Nevada, Clark Co., Cottonwood Spring, *Bailey et al. 1884* (US, holotype).

Glabrous or tomentose plants; lower leaves ovate to ovate-lanceolate. Southern California, southern Nevada, and northeastern Arizona.

8b. Amsonia tomentosa var. **stenophylla** Kearney and Peebles, J. Wash. Acad. Sci. 29:487. 1939. TYPE: United States, Arizona, Navajo Co., Monument Valley, *Peebles and Fulton 11944* (US, holotype).

A. arenaria Standl., Proc. Biol. Soc. Wash. 26:117. 1913. TYPE: United States, Texas, El Paso Co., sand hills between Strauss and Anapra, *Stearns 372* (US, holotype).

A. eastwoodiana Rydb., Bull. Torrey Bot. Club 40:465. 1913. Nomen ambiguum.

A. filiformis Nels., Am. J. Bot. 18:433. 1931. TYPE: Mexico, Chihuahua, near Lake Guzman, *Pringle 6796* (RM, holotype; GH, MO, RSA, isotypes).

Glabrous or tomentose plants; lower leaves lanceolate to linear-lanceolate. Utah, northern Arizona, southern New Mexico, west Texas and northern Chihuahua.

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A SYNOPSIS OF *MORAEA* (IRIDACEAE) WITH NEW TAXA, TRANSFERS, AND NOTES[1]

PETER GOLDBLATT[2]

ABSTRACT

A synopsis of *Moraea*, a genus of African Iridaceae is presented. This summarizes, in systematic sequence, the subgenera, sections and species from revisions published over a period from 1973–1977, covering the genus over its entire range. The synopsis includes all taxonomic changes made in the later revisions and places the four species of *Moraea* transferred here from *Homeria* in 1980. Six new species, *M. linderi, M. flexuosa, M. vallisavium, M. longiaristata, M. atropunctata,* and *M. calcicola* and one new subspecies, *M. villosa* subsp. *elandsmontana* are described; *M. robusta* is raised from subspecies status in *M. galpinii*.

INTRODUCTION

Moraea is a large genus of Iridaceae-Iridoideae restricted to sub-Saharan Africa. It is concentrated in montane areas in the tropics but occurs at all altitudes in southern Africa. It is best represented in the winter rainfall area of southern Africa where all of the five subgenera and over half the species occur. Currently, some 98 species are recognized, a further six are described here and one subspecies is elevated to species rank, making a total of 105. The genus has been revised recently in three parts, divided geographically: the treatment for species of the summer rainfall part of southern Africa was published first (Goldblatt, 1973), then that for the winter rainfall area (Goldblatt, 1976b), followed by tropical Africa (Goldblatt, 1977). Few species are shared by more than one region, but some overlaps occur and some changes were made in later revisions for species treated earlier. In addition, several species previously assigned to *Homeria* were transferred to *Moraea* (Goldblatt, 1979, 1980) as a result of critical biosystematic and cytological studies.

Other significant changes, published elsewhere, include the reduction to synonymy of the subspecies of *M. spathulata* (Goldblatt, 1977); placement of *M. bellendenii* subsp. *cormifera* in *M. tricuspidata* (Goldblatt, 1976b), and the application of the name *M. polyanthos* to a species previously known as *Homeria*

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lilacina so that the species long known by that name must be called *M. bipartita* (Goldblatt, 1979).

It now seems an appropriate time to summarize the accumulated changes to the taxonomy of *Moraea* in a synposis of the whole genus. Species are ordered (Table 1) in a sequence that is, to the degree possible in a linear arrangement, phylogenetic, and wherever possible related species are placed close together. The subgenera and sectional treatment follows the system established by Goldblatt (1976a).

NOTES

There are minor changes in the system. *Moraea nubigena,* a dwarf, much reduced alpine species, is removed from subgenus *Vieusseuxia* to subgenus *Moraea,* next to *M. lugubris* in section *Moraea*. *Moraea nubigena* was unknown cytologically when originally described (Goldblatt, 1976b), but a chromosome count of $2n = 20$, obtained recently has (Goldblatt, in prep.) indicated that its correct placement is in subgenus *Moraea*.

A correction must be made to the published distribution information for *Moraea caeca* which was treated as occurring on the Cape Peninsula on Karbonkelberg (Goldblatt, 1976b). Recently, I was shown specimens collected here (*Malan sub Goldblatt 5922*) that were clearly *M. tricuspidata,* unusual only in having purple instead of white flowers. This collection matches *Salter 3288,* the specimen misidentified as *M. caeca,* from the same locality. The disjunction in the range of *M. caeca* between the Piketberg–Porterville Mts. and Cape Peninsula is thus incorrect. The description of *Moraea tricuspidata* must now be expanded to include this purple-colored form. The known range of this species has also been extended to the Cedarberg, where I have collected specimens, growing locally at the edge of a vlei and blooming after a veld fire (*Goldblatt 5129*).

NEW TAXA AND COMBINATIONS

SUBGENUS *MORAEA*

SECTION *MORAEA*

1. **Moraea linderi** Goldbl. sp. nov. TYPE: South Africa, Cape, Piketberg Mts., Moutons Hoek, *Linder 638* (MO, holotype).

Planta 35–45 cm alta, cormo ca. 18 mm in diametro, multos bulbilos a base ferenti, tunicis brunneis, primis integris, ultimis fibrescentis, foliis 3, inferiore basali manifeste unifaciali vel tereti, foliis superioribus congestis, multum supra terram insertis, canaliculatis, spathis 3.5–4 cm longis, exteriore apice libro, flore pallido flavo, tepalis exterioribus ca. 35 mm longis, interioribus grandioribus, filamentis manifeste libris, ramis styli 12 mm longis, cristis ca. 10 mm longis, prominentibus.

Plants 35–45 cm high. *Corm* ca. 18 mm in diameter, bearing numerous pale cormlets at base, tunics brown, initially unbroken, breaking from below into sections and becoming fibrous eventually, older, outer layers partly fibrous. *Cataphyll* membranous. *Leaves* 3, lowermost basal, upright or curving outward, evidently unifacial but perhaps terete when live, second and third leaves inserted well above ground, and close together, 10–20 cm long, channelled, up to 4 mm wide. *Stem* erect, branching well above-ground, and branches closely set, few branched. *Spathes* 3.5–4 cm long, herbaceous, brown-tipped, truncate to acute, outer spathe leaf-like and with free apex, shorter to exceeding inner spathe.

TABLE 1. Synopsis of *Moraea*. Species marked with an asterisk (*) are described in this paper for the first time.

SUBGENUS *MORAEA*

SECTION *MORAEA*

1. *M. ramosissima* (L. f.) Druce—SW and Southern Cape to Grahamstown
2. *M. gawleri* Spreng.—Namaqualand, SW and Southern Cape
3. *M. vegeta* L.—SW Cape
4. *M. indecora* Goldbl.—Northern Namaqualand
5. *M. papilionacea* (L. f.) Ker—SW Cape
6. *M. fergusoniae* L. Bol.—Southern Cape
*7. *M. linderi* Goldbl.—Piketberg, SW Cape
8. *M. margaretae* Goldbl.—Namaqualand
9. *M. serpentina* Baker—Namaqualand
10. *M. tortilis* Goldbl.—Namaqualand
11. *M. nubigena* Goldbl.—Brandwacht Mts., SW Cape
12. *M. lugubris* (Salisb.) Goldbl.—SW Cape

SECTION *ACAULES* (Baker, 1896)

13. *M. falcifolia* Klatt—Namaqualand, Karoo, dry parts of SW Cape
14. *M. ciliata* (L. f.) Ker—Namaqualand, SW Cape to Eastern Cape, and local in the Karoo
15. *M. macronyx* Lewis—SW and Southern Cape
16. *M. tricolor* Andrews—SW Cape

SECTION *DESERTICOLA* (Goldblatt, 1976a)

17. *M. saxicola* Goldbl.—Namaqualand
18. *M. macgregorii* Goldbl.—Southern Namaqualand
19. *M. namibensis* Goldbl.—Southwestern Namibia
20. *M. bolusii* Baker—Namaqualand

SECTION *SUBRACEMOSAE* (Baker, 1896)

21. *M. gracilenta* Goldbl.—Western Cape
22. *M. fugax* (de la Roche) Jacq.—Namaqualand to SW Cape

SECTION *TUBIFLORA* (Goldblatt, 1976a)

23. *M. cooperi* Baker—SW Cape
24. *M. longiflora* Ker—Kamiesberg, Namaqualand

SECTION *FLEXUOSA* (Goldblatt, this paper)

*25. *M. flexuosa* Goldbl.—Anenous flats, Richtersveld

SUBGENUS *VISCIRAMOSA* (Goldblatt, 1976a)

26. *M. bubalina* Goldbl.—Northwestern Cape
27. *M. bituminosa* (L. f.) Ker—SW Cape
28. *M. viscaria* (L. f.) Ker—SW Cape
29. *M. inconspicua* Goldbl.—Namaqualand to Humansdorp, Southern Cape
30. *M. elsiae* Goldbl.—SW Cape

SUBGENUS *MONOCEPHALAE* (Goldblatt, 1976a)

31. *M. angusta* (Thunb.) Ker—SW and Southern Cape
32. *M. anomala* Lewis—SW Cape
*33. *M. vallisavium* Goldbl.—Klein River Mts., Caledon district, SW Cape
34. *M. neglecta* Lewis—SW Cape

SUBGENUS *VIEUSSEUXIA* (Baker, 1892)

SECTION *POLYANTHES* (Goldblatt, 1976a)

35. *M. bipartita* L. Bol.—Little Karoo, Southern and E Cape
36. *M. polyanthos* L. f.—Little Karoo and Southern Cape
37. *M. crispa* Thunb.—Karoo, Roggeveld and Cedarberg
38. *M. polystachya* (Thunb.) Ker—Karoo, E and N Cape, W Orange Free State, S and Central Namibia
39. *M. speciosa* (L. Bol.) Goldbl.—Western Karoo
40. *M. carsonii* Baker—Zimbabwe, Zambia, Malawi, S Tanzania and S Zaire
41. *M. callista* Goldbl.—Southern Highlands, Tanzania

TABLE 1. Continued.

42. *M. afro-orientale* Goldbl.—East Africa, S Sudan
43. *M. iringensis* Goldbl.—Southern Highlands, Tanzania
44. *M. natalensis* Baker—Zimbabwe, Zambia, Malawi and E South Africa
45. *M. elliotii* Baker—E Cape, Natal, Transvaal and Malawi
46. *M. inclinata* Goldbl.—Drakensberg, Natal, Transkei
47. *M. thomsonii* Baker—E Cape through tropical central Africa to Ethiopia
48. *M. alpina* Goldbl.—Drakensberg, Natal and Lesotho

SECTION *THOMASIAE* (Goldblatt, 1976a)

49. *M. thomasiae* Goldbl.—Worcester to Little Karoo

SECTION *VIEUSSEUXIA*

50. *M. algoensis* Goldbl.—Little Karoo and Southeastern Cape to Port Elizabeth
51. *M. tripetala* (L. f.) Ker—Southwestern Cape, Roggeveld and Southern Cape to George
52. *M. debilis* Goldbl.—Caledon district, SW Cape
53. *M. incurva* Lewis—Wellington district, SW Cape
*54. *M. longiaristata* Goldbl.—Caledon Zwartberg, SW Cape
55. *M. barnardii* L. Bol.—Caledon district, SW Cape
56. *M. barkerae* Goldbl.—Cedarberg Mts., SW Cape
57. *M. unguiculata* Ker—Namaqualand, SW Cape, Southern Cape and Mts. of the Karoo
58. *M. trifida* Foster—Drakensberg, Transkei, Natal, Lesotho to S Transvaal
59. *M. marionae* N. E. Br.—Transvaal-Swaziland escarpment and Mts. and Zululand
60. *M. pubiflora* N. E. Br. subsp. *pubiflora*—E Transvaal and Swaziland
subsp. *brevistyla* Goldbl.—Natal, Lesotho, Transkei
61. *M. albicuspa* Goldbl.—Southern Drakensberg, Natal, and Transkei
62. *M. dracomontana* Goldbl.—Drakensberg, Natal and Lesotho
63. *M. modesta* Killick—E Transvaal, Natal, Lesotho, and Transkei
64. *M. tricuspidata* (L. f.) Lewis—SW through Southern Cape to Grahamstown
65. *M. bellendenii* (Sweet) N.E. Br.—SW and Southern Cape
66. *M. lurida* Ker—Caledon district to Bredasdorp, SW Cape
67. *M. insolens* Goldbl.—Caledon district, SW Cape
*68. *M. atropunctata* Goldbl.—Eseljacht Mts., SW Cape
69. *M. neopavonia* Foster—Western Cape
70. *M. gigandra* L. Bol.—Piketberg district, SW Cape
71. *M. caeca* Goldbl.—Piketberg district, SW Cape
72. *M. aristata* (de la Roche) Asch. & Graeb.—Cape Peninsula
73. *M. amissa* Goldbl.—Malmesbury district, SW Cape
74. *M. villosa* (Ker) Ker subsp. *villosa*—SW Cape
* subsp. *elandsmontana* Goldbl.—Elandkloof Mts., S of Gouda
75. *M. tulbaghensis* L. Bol.—Tulbagh district to Gouda, SW Cape
*76. *M. calcicola* Goldbl.—Saldanha district, SW Cape
77. *M. loubseri* Goldbl.—Langebaan, SW Cape

SUBGENUS *GRANDIFLORA* (Goldblatt, 1976a)

78. *M. moggii* N. E. Br. subsp. *moggii*—N and E Transvaal
subsp. *albescens* Goldbl.—SE Transvaal
79. *M. muddii* N. E. Br.—E Cape to E Zimbabwe and Mozambique
80. *M. unibracteata* Goldbl.—Natal Midlands
81. *M. inyangani* Goldbl.—Inyanga Mts., Zimbabwe
82. *M. angolensis* Goldbl.—S Angola
83. *M. carnea* Goldbl.—Drakensberg, Natal
84. *M. ardesiaca* Goldbl.—Drakensberg, Natal
85. *M. graminicola* Oberm. subsp. *graminicola*—Natal Midlands to coast
subsp. *notata* Goldbl.—Transkei
86. *M. galpinii* (Bak.) N. E. Br.—E Transvaal, N Natal
*87. *M. robusta* (Goldbl.) Goldbl.—E Transvaal, N Natal, Transkei
88. *M. hiemalis* Goldbl.—Natal Midlands
89. *M. reticulata* Goldbl.—Winterberg Mts., E Cape
90. *M. spathulata* (L. f.) Klatt—S Cape to E Zimbabwe and Mozambique
91. *M. alticola* Goldbl.—Drakensberg, Natal and Lesotho
92. *M. huttonii* (Bak.) Oberm.—Drakensberg, Natal, Lesotho to NE Cape
93. *M. schimperi* (Hochst.) Pic-Serm.—Zimbabwe and Angola north to Ethiopia and east to Nigeria

TABLE 1. Continued.

94. *M. bella* Harms—S Tanzania, Malawi, N Mozambique, Zambia and S Zaire
95. *M. verdickii* De Wild.—E Angola, Zambia, Zaire, Malawi, S Tanzania and Mozambique
96. *M. macrantha* Baker—Malawi, E Zambia and S Tanzania
97. *M. ventricosa* Baker—Zambia, Zaire, Burundi and S Tanzania
98. *M. textilis* Baker—Angola and W Zambia
99. *M. tanzanica* Goldbl.—S Tanzania and Malawi
100. *M. brevifolia* Goldbl.—Zambia
101. *M. clavata* Foster—Angola and Zambia
102. *M. upembana* Goldbl.—S Zaire
103. *M. bovonei* Chiov.—S Zaire
104. *M. balundana* Goldbl.—S Zaire
105. *M. unifoliata* Foster—S Zaire

Flower evidently pale yellow; *outer tepals* ca. 35 mm long, claw ca. 15 mm, ascending, limb horizontal, ?12 mm wide; *inner tepals* ?2.5 mm long, possibly erect, ca. 4 mm at widest point. *Filaments* 8 mm long, evidently entirely free but contiguous for 2–3 mm, diverging above, *anthers* 6 mm long. Ovary ca. 7 mm long, *style* branches 12 mm long, ca. 3 mm wide, crests prominent ca. 10 mm long. *Capsule* and seeds unknown. *Chromosome number* unknown.

Flowering time: December.

Distribution: known only from one site in the Piketberg Mts., in sandy Cape mountain soil.

This species was recently discovered by Peter Linder during a survey of the flora of the Piketberg Mountains, and it is named in his honor. *Moraea linderi* is evidently rare and so far is known only from the type locality. Like many geophytes of the Cape mountain flora, it probably only flowers well after burning or clearing and it may be more common than the present record indicates.

Moraea linderi is an unusual species; with its several leaves and branches, and apparently free filaments it seems to be one of the most primitive species of the genus. The brown, initially entire, corm tunics, although rare in *Moraea*, are also found in the Namaqualand species, *M. margaretae* (Goldblatt, 1976b) as well as in the genus *Rheome*, which was recently segregated from *Homeria* (Goldblatt, 1980), and in *Hexaglottis nana*. It is not clear whether the possession of this distinctive type of corm tunic indicates a close relationship between these species, presently placed in three different genera, but this possibility will be investigated in the near future.

The similarity in vegetative morphology between *Moraea linderi* and *Rheome umbellata* is particularly marked. Except for the presence of a basal leaf in *M. linderi*, the two species cannot be distinguished. The flowers, however, differ markedly. *Moraea linderi* has a typical *Moraea* type of flower, with unequal inner and outer tepals, large petaloid style branches and prominent crests, while *R. umbellata* has subequal inner and outer tepals and narrow style branches without crests. It seems likely that *Rheome umbellata* may have been derived from *M. linderi* by the same pattern of floral simplification and reduction evident in *Moraea polyanthos* (Goldblatt, 1980) and in other species groups in *Moraea*, which has resulted in the independent development of this *Homeria* type flower repeatedly.

SOUTH AFRICA: Cape 3218 (Clanwilliam) Piketberg Mts, Moutons Hoek (DC), *Linder 638* (MO).

SECTION *FLEXUOSA*

Section **Flexuosa** Goldbl. sect. nov. TYPE and only species: *Moraea flexuosa* Goldbl.

Folia 3–5, canaliculatis, caule flexuoso, tunicis cormi fibrosis, nigrescentibus, apicibus spathae exterioris libris arcuatisque, filamentis connatis, libris ad apicem, ramis styli petaloideis, cristis productis, numero chromosomato $x = 6$.

2. Moraea flexuosa Goldbl. sp. nov. TYPE: South Africa, Cape, Richtersveld, Eksteenfontein road, *Goldblatt 6000A* (MO, holotype, K, NBG, PRE, S, WAG, isotypes).—FIG. 1.

Planta parva ad 10 cm alta, tunicis cormi fibrosis, nigrescentibus, foliis 3–5, canaliculatis, ad 6 cm longis, caule flexuoso, simplice ad 4-ramoso, spatha 2.5–4 cm longa, exteriore ad 10 mm breviore, apicibus libris et arcuatis, flore flavo, tepalis exterioribus 28–30 mm longis, unguibus ca. 16 mm longis, columna filamentarum 11–12 mm longa, libra ad apicem, antheris ca. 3.5 mm longis.

Plants 6–10 cm high. *Corm* 10–15 mm in diameter, tunics of matted, coarsely reticulate, dark brown (–black) fibers. *Cataphyll* solitary, dry, membranous, pale or light brown. *Leaves* 3–5, lowermost inserted shortly, to 2 cm above the ground and largest, upper leaves progressively shorter, all falcate, channeled, to 6 cm long, 3–6 mm wide, grey-green. *Stem* flexuose, sharply flexed above sheathing base of each leaf, simple or with up to 4 branches. *Spathes* herbaceous, acuminate, 2.5–4 cm long, outer about as long to 10 mm shorter, sheathing below only, upper half to two-thirds free and curved outwards. *Flower* pale yellow, inner and outer tepals deeper yellow toward base of tepal limb, with nectar guides on outer tepals only, consisting of numerous small dark green dots, weakly scented; *outer tepals* 28–30 mm long, claw erect, limb horizontal, 12 mm long, 8 mm wide; inner tepals 25–27 mm long, claw narrow, curving outward, limb ca. 12 mm long, 7 mm wide, horizontal, blade twisted through 45°. *Filaments* 11–12 mm long, united in a cylindrical column, free in upper ca. 1.5 mm and curved outward; *anthers* appressed to style branches, straight, ca. 3.5 mm long, white. Ovary ca. 7 mm long, reddish; *style* dividing at apex of filament column, branches 4 mm long; *crests* ca. 2 mm long, erect. *Capsule* oblong, 12–15 mm long. *Chromosome number* $2n = 12$ (*Goldblatt 5742*).

Flowering time: July–early August.

Distribution: local in fine sandy loess on flats in the southern Richtersveld.—Fig. 1.

This very distinct new species was discovered only in 1979 by N. J. van Berkel, while working with her husband prospecting in northern Namaqualand. Photographs taken in the field and later shown to me indicated that this was a very unusual and undescribed *Moraea*. Visits in the two following years to the area where the plants were found revealed that this species has a very localized distribution, no more than a few acres in extent in fine sandy loess, on the plains below Anenous Pass. The species is very early blooming, usually in July, and possibly even earlier. Plant growth is very rapid, and the first flowers are produced three to four weeks after the first soaking autumn or winter rains fall in this arid area of the west coast of southern Africa.

Both vegetative and floral morphology are unusual, but the overall impression is that *Moraea flexuosa* is derived from a fairly unspecialized group within the genus. Its quite generalized flower is unusual mainly in the tepals having very

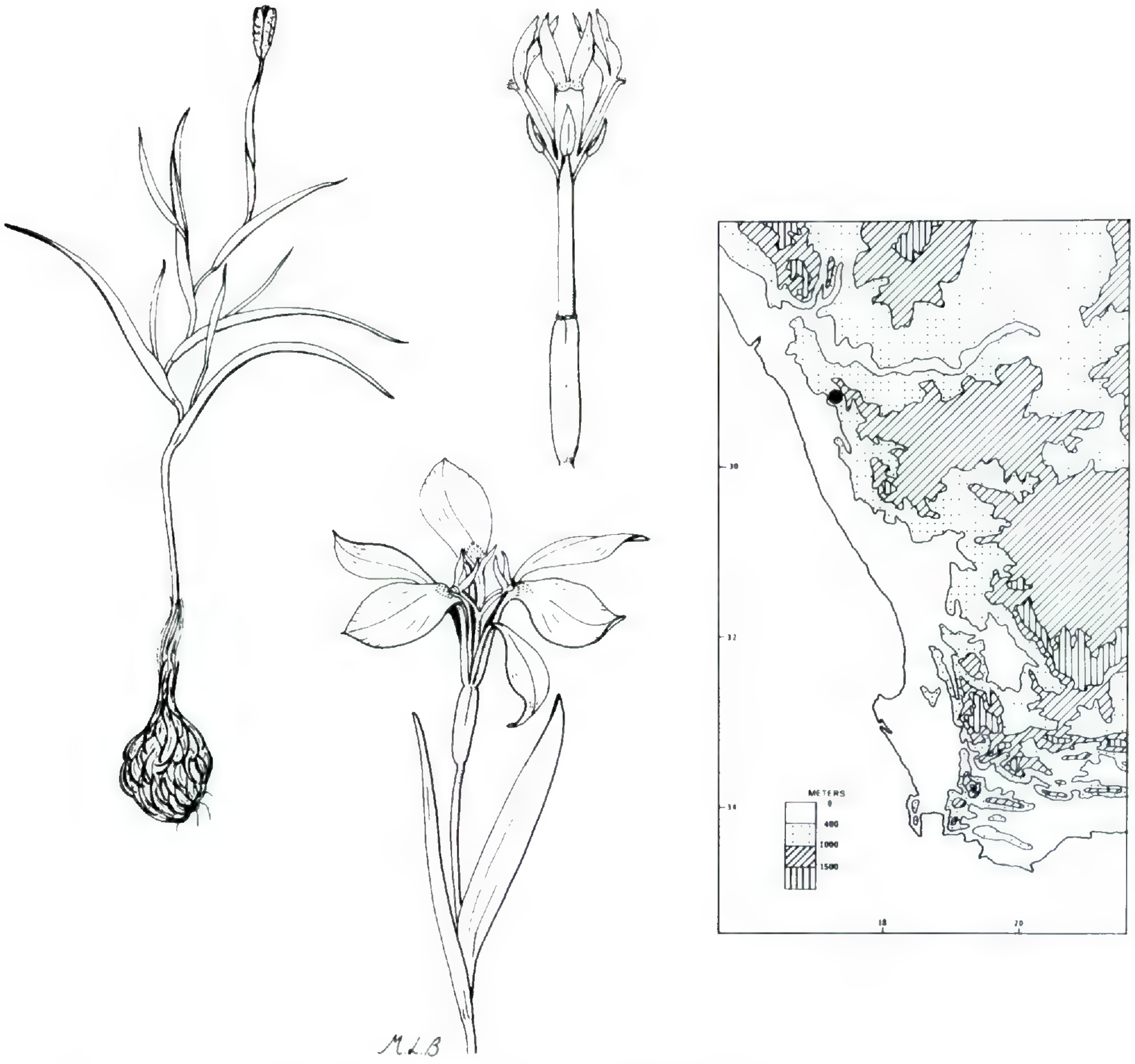

FIGURE 1. Morphology and distribution of *Moraea flexuosa* and distribution of *Moraea linderi*. Habit ×0.5; flower ×1; detail of ovary, stamens, and style branches ×2.

long claws, and the filaments are united to a greater extent than is usual in the genus. The several-leafed character is consistent with a placement in subgenus *Moraea,* but it is so unusual here in its flower and in chromosome number of $2n = 12$ (in contrast to the base of $x = 10$ in the subgenus) that it is assigned to its own section. The karyotype, consisting only of acrocentric chromosomes, is remarkably similar to that found in *Homeria,* a genus closely allied to *Moraea* but having different floral morphology. It seems reasonable to speculate that *M. flexuosa* may be close to the line that gave rise to *Homeria*.

SOUTH AFRICA: Cape 2917 (Springbok) Eksteenfontein road, ca. 6 km N of Port Nolloth road, farm Kootjesvlei, sandy loess soil (AB), *Goldblatt 5742* (K, MO, NBG, PRE, S, WAG), *6000* (MO), *6000A* (K, MO, NBG, PRE, S, WAG), *Van Berkel 93* (MO).

SUBGENUS *MONOCEPHALAE*

3. **Moraea vallisavium** Goldbl. sp. nov. TYPE: South Africa, Cape, Vogelgat, Hermanus, mountain slopes, 1,500 ft, *Goldblatt 5394* (MO, holotype; K, NBG, isotypes).—FIG. 2.

Planta ad 10–34 cm alta, cormo 4–6 mm in diametro veteribus persistentibus, tunicis fibrosis reticulatis, folio solitario lineari unifaciali caule excedenti 1–2 mm lato, caule bractea una vaginati marginibus liberis, marginibus spathae exterioris liberis, apicibus spatharum obtusis vel truncatis, floribus luteis, limbis tepalorum horizontalibus vel pauce reflexis, tepalis exterioribus 20–24 mm longis, interioribus 16–19 mm longis, filamentis ca. 5 mm longis connatis infra, ramis styli 8 mm longis, ad 4 mm latis, capsula angusta turbinata, seminibus fusiformibus.

Plants 10–34 cm high. *Corm* small, 4–6 mm in diameter, with corms of past seasons persisting below, tunics of fine reticulate fibers. *Cataphyll* pale, membranous, becoming fibrous and accumulating around the base in a neck. *Leaf* solitary, linear, unifacial, inserted above ground level, 1–2 mm wide, exceeding the stem and arching over to trailing. *Stem* more or less erect to inclined, unbranched, bearing a single sheathing bract 15–40 mm long with margins free to base. *Spathes* 3–4 mm long, herbaceous, obtuse to truncate, outer about half as long as inner and with margins free to base. *Flower* yellow, tepals with claws darkly speckled, the outer with deep yellow nectar guides at base of limbs; *outer tepals* 20–24 mm long, claw ascending, 9–10 mm long, limb horizontal to slightly reflexed, limb 8–10 mm wide; *inner tepals* 16–19 mm long, claw 6–8 mm long, limb to 7 mm wide, also horizontal to slightly reflexed. *Filaments* ca. 5 mm long, united in lower 2 mm; *anthers* 5–6 mm long, reaching to the apex of the style branches, pollen red. Ovary 8–10 mm long, triangular in section, *style branches* ca. 8 mm long, about 4 mm wide, crests 6–10 mm long, erect. *Capsule* narrowly turbinate, somewhat triangular, 12–17 mm long, dehiscent in upper third, seeds spindle shaped, 2 mm long and ca. 1 mm wide. Chromosome number unknown.

Flowering time: late December to January.

Distribution: Klein River Mountains, known only from Vogelgat east of Hermanus, in damp sites, often on steep south facing slopes.—Fig. 2.

Moraea vallisavium is an unusual and apparently rare species, occurring in the mountains of the Caledon district. It has seldom been collected, probably owing to the fact that it blooms in summer and at relatively high altitudes and also because it has the habit of blooming well only after a fire the previous summer, although in rocky or cleared sites it will bloom year after year.

The species is unusual in several features. The corm tunics are finely fibrous and reticulate, a very rare characteristic in *Moraea,* and the older season's corms persist, accumulating below the current corm. The leaves seem unique in *Moraea* in being flat and monofacial rather than bifacial and channeled as is most frequent in the genus or terete as in its apparent relatives in subgenus *Monocephalae.* Also unusual are the margins of the sheathing bract and outer spathe, which are free to the base instead of being partly united. Fibrous corm tunics in genera where less broken tunic layers are the rule, sometimes occur in high mountain species, especially those of damp sites, and persistent old corms are also occasionally found in montane species in other genera of Iridaceae and these two characteristics may be derived rather than primitive as they at first appear. However, the monofacial leaf, unknown elsewhere in *Moraea* except perhaps in the recently discovered and incompletely known *M. linderi* also described in this paper, seems a truly primitive characteristic, as are the free margins of the sheathing bract and outer spathe valve. The solitary leafed and unbranched habit are, in contrast, specialized characteristics of *Moraea*. *Moraea vallisavium* thus has a curious combination of unusual, and both primitive and derived characteristics.

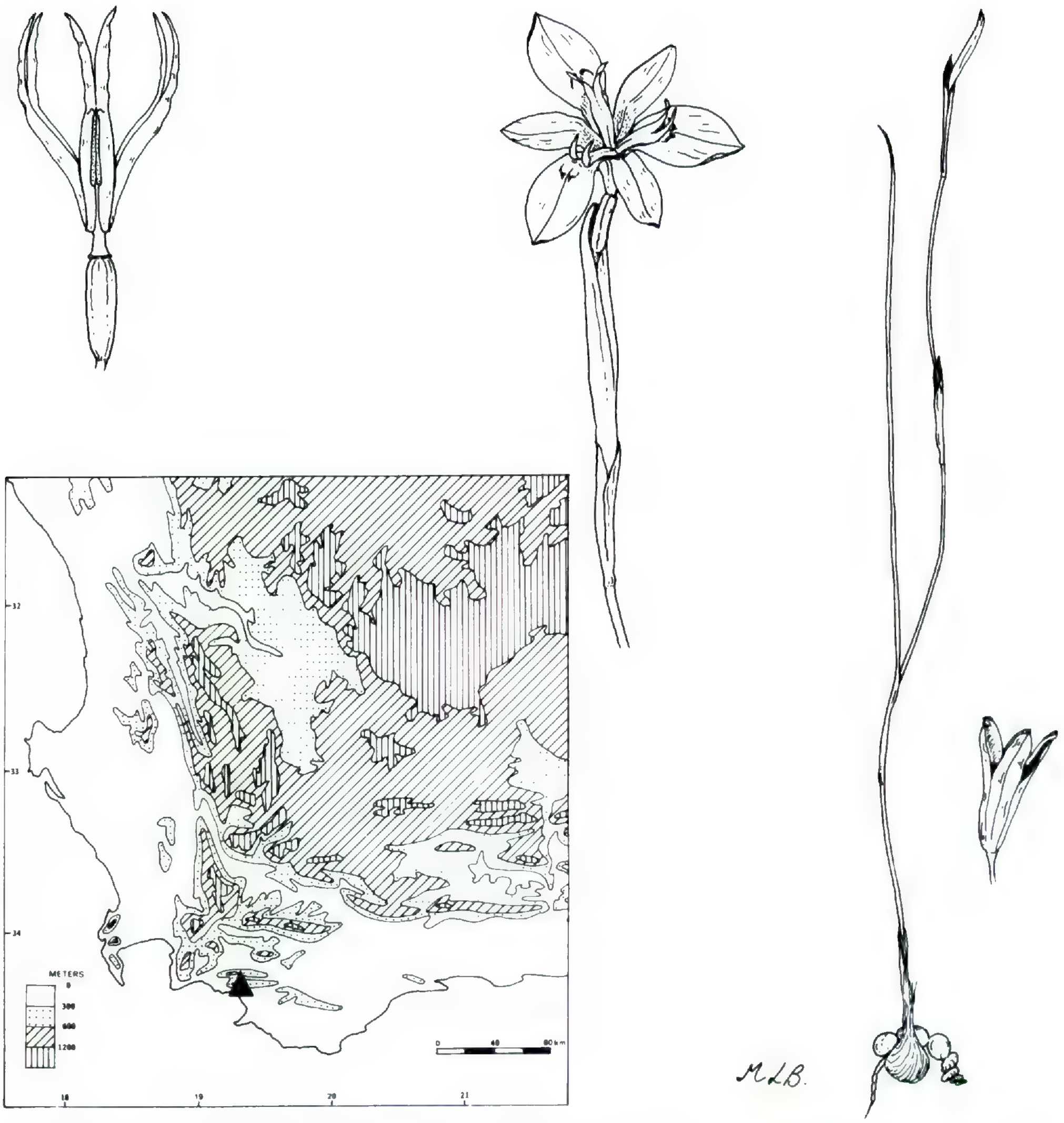

FIGURE 2. Morphology and distribution of *Moraea vallisavium*. Habit, flower, and capsule ×1; stamens and style branches ×1.5.

Moraea vallisavium seems to be most closely related to *M. angusta* and to *M. anomala*, with which I initially associated it. These are closely related members of subgenus *Monocephalae*, all three species of which have in common a single, terete leaf, unbranched stem and fairly large yellow to cream flowers. The fruits of all three species are unmistakable in *Moraea*, being ovoid to rotund and relatively short while the seeds are flat and thin, lying horizontally in the locules of the capsule. Dry, old capsules of *M. vallisavium* that I collected with the current season's growth in 1979 seemed different in being rather slender, but since all the seed has been shed they could not be examined when I first collected the species. Only in 1982 was a complete capsule found by Ion Williams, owner of the Vogelgat Native Reserve after repeated searches at the known sites for the species. The capsules are clearly slender and narrowly turbinate, while the seeds

are spindle-shaped, relatively large for *Moraea* and quite unlike the flattened discoid seeds of other species of subgenus *Monocephalae*. The nature of the fruits convinced me that I was dealing with a distinct species rather than merely an unusual form of *M. anomala* or the related *M. angusta* with small flowers, atypical corms and corm tunics. However, *M. vallisavium* does seem to belong in subgenus *Monocephalae* with which its single leaf inserted above the ground, unbranched stem, and generalized flower conform. Also the margins of the sheathing bract and outer spathe are nearly free in the other species of the subgenus, so it appears that in this feature *M. vallisavium* is not particularly unusual. It is difficult to determine whether its flat, unifacial leaf is truly primitive or a secondary modification of the terete leaf, characteristic of subgenus *Monocephalae*. In fact, in dried material it is not even possible to determine that the leaves of members of subgenus *Monocephalae* were originally flat and unifacial or terete.

Moraea anomala, which has the smallest flowers of the three recognized species of subgenus *Monocephalae,* has outer tepals in the 30–45 mm long range, filaments 6–14 mm long and anthers 4–8 mm long (Goldblatt, 1976b). It almost always has two sheathing bracts on the stem and blooms from September to November at higher elevations. In contrast, *M. vallisavium* has outer tepals only 20–24 mm long, filaments ca. 5 mm long and anthers 5–6 mm long. It is recorded as blooming from late December into January and all specimens have only one stem bract. It thus seems reasonably distinct from *M. anomala* in floral characters as well as in the fruits and seed. *Moraea angusta* usually has large flowers, with outer tepals in the 30–50 mm range, filaments 5–15 mm long, joined only near the base, and anthers normally 7–10 mm long. However, some high altitude collections assigned to the species, notably *Wurts 496* from Eleven O'Clock Mt. at Swellendam, and a recent collection, *Esterhuysen 35606,* made in 1981 in the same area have smaller flowers with outer tepals 22–25 mm long, filaments ca. 6 mm long and anthers ca. 4 mm long. These specimens are easily confused with *M. vallisavium* especially as they are late blooming, November to January and have fibrous corm tunics (corms lacking in the Wurts gathering). The Esterhuysen collection has nearly ripe capsules, and these are rotund, and quite typical of *M. angusta*. It seems, then, that *M. vallisavium* lies close to both *M. anomala* and *M. angusta* but differs from both mainly in its fruits and seed characters, although it can be distinguished from most collections of these species by its corm tunics and flowers as well.

SOUTH AFRICA: Cape 3419 (Caledon) Vogelgat Nature Reserve, 1,600 ft, damp area in path between Vulture and Beaconhead Streams (AD), *Goldblatt 5398* (MO); Vogelgat, S facing cliff, above Fence Stream in peaty soil, 1,500 ft, *Goldblatt 5347* (MO), *5394* (K, MO, NBG); north side of Fence Stream, Vogelgat/Diepgat, at base of steep shady cliff, 490 m, *Williams 3200* (MO).

SUBGENUS *VIEUSSEUXIA*
SECTION *VIEUSSEUXIA*

4. **Moraea longiaristata** Goldbl. sp. nov. TYPE: South Africa, Caledon Zwartberg, above Caledon Garden, *Goldblatt 5883* (MO, holotype, C, E, K, NBG, PRE, S, US, WAG, isotypes).—FIG. 3.

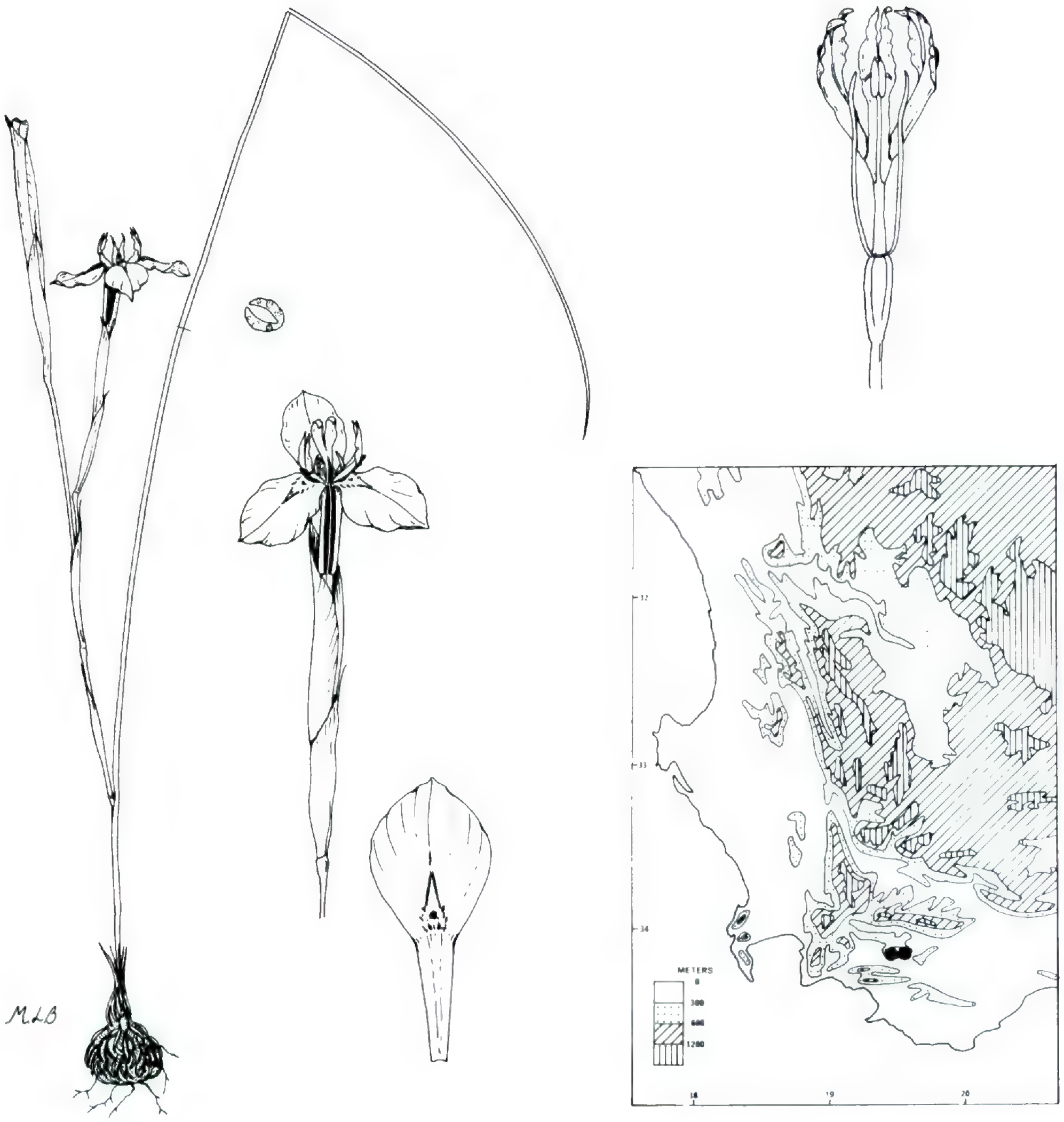

FIGURE 3. Morphology and distribution of *Moraea longiaristata*. Habit ×0.5; flower ×1; outer tepal and detail of ovary, inner tepals, stamens, and style branches ×2.

Planta 15–30 cm alta, tunicis cormi pallidis brunneis, folio unico, basali, canaliculato, caulem excedente, caule simplice raro uniramoso, spathis 4.5–5.5 cm longis, interiore duplo longiore exteriore, flore albo, caeruleo maculato, limbis tepalorum exteriorum 11–14 mm longis, unguibus 11–16 mm longis, tepalis interioribus aristatis, ± erectis, ad 2.5 cm longis, filamentis 12–15 mm longis, connatis in parte inferiore, antheris 3–4 mm longis, ramis styli ca. 10 mm longis, cristis ca. 5 mm longis.

Plants 15–30 cm high. *Corm* 8–12 mm in diameter, tunics of pale, coarse fibers. *Leaf* solitary, basal, channelled, erect, longer than stem, often dry toward apex, ca. 2 mm wide. *Stem* erect, simple, occasionally bearing one branch, stem bracts 2, 3–4 cm long, apices dry, attenuate. *Spathes* 4.5–5.5 cm long, outer about half the inner. *Flower* white with blue spots near base of outer tepal limbs; *outer tepals* 23–30 mm long, claw 12–16 mm, erect, limb spread horizontally to slightly

reflexed, shorter than claw, 11–16 mm wide, margins undulate; *inner tepals* 13–15 mm long, aristate, erect, curving inward toward apex. *Filaments* 12–15 mm long, united for lower 6–7 mm; *anthers* red, 3–4 mm long. Ovary 8–10 mm long, entirely or partly enclosed in spathes; *style branches* ca. 10 mm long; *crests* erect, ca. 5 mm long. *Capsule* and seeds unknown. *Chromosome number* unknown.

Flowering time: September to mid-October.

Distribution: stony sandstone soils of the Caledon Zwartberg, especially in cleared or burned situations.—Fig. 3.

Moraea longiaristata has been known since at least the late nineteenth century when it was collected by H. Bolus but it has until now been confused with *M. tripetala,* which it resembles closely when dry and poorly pressed. The few dry specimens available to me when studying *Moraea* in the winter rainfall area were assigned to *M. tripetala*. Only when I saw the live specimens at the Caledon Wild Flower Show placed together with *M. tripetala* and then in the field did it become clear that this was a distinct species.

It is obviously closely allied to *Moraea barnardii,* a species also endemic to the Caledon district and occurring on the mountains a few miles to the south, across the Caledon flats. Both *M. longiaristata* and *M. barnardii* have a similar habit and flower, but on examination the flowers are structurally quite different. *Moraea longiaristata* has very long cusp-like inner tepals, ca. 15 mm long, and outer tepals with long claws 12–16 mm long. In contrast, *M. barnardii* lacks inner tepals entirely, and the outer tepal claws are quite short, ca. 7 mm long. The filaments of *M. longiaristata* are extended in proportion to the tepal claws, and are up to 15 mm long, whereas in *M. barnardii* the filaments are only 8–9 mm long. In other respects, including shape, color, and orientation of outer tepal limb, anther shape and color, and style branch and crest morphology, the two species are apparently identical. The several, quite striking similarities suggest that *M. longiaristata* and *M. barnardii* are recent derivatives of a common ancestor.

Moraea longiaristata grows in typical, coarse Cape Sandstone derived soil, on south trending slopes and is most common in very stony situations. It is restricted to the Caledon Zwartberg.

SOUTH AFRICA: Cape 3419 (Caledon) Caledon (AB), *Rogers s.n.* (K.); near Caledon, *H. Bolus s.n.* (BOL 7878); hills near Caledon, *H. Bolus s.n.* (BOL 9169); Swartberg, *Esterhuysen 18932* (BOL); Caledon Zwartberg, slopes above Caledon Garden, *Goldblatt 5883* (C, E, K, MO, NBG, PRE, S, US, WAG); Caledon Zwartberg slopes, ca. 1,500 ft, *Goldblatt 5898* (MO); 2 km E of Caledon, below main road, *Goldblatt 5914* (BOL, MO); farm Paarde Valley, NE side of Caledon Zwartberg (BA), *Burghers 2807* (STE).

5. **Moraea atropunctata** Goldbl. sp. nov. TYPE: South Africa, Caledon dist., Vleitjies farm, Eseljacht Mts., *Goldlbatt 5635* (MO, holotype, K, NBG, PRE, S, US, isotypes).—FIG. 4.

Planta 15–20 cm alta, tunicis cormi pallidis brunneis, folio unico, canaliculato, basali, 4–8 mm lato, marginibus ciliato-pubescentibus, caule glabro, simplice vel uniramoso, spathis 4.5–6.5 cm longis, exteriore duplo longiore interiore, flore cremei-albo, brunneo reverso, brunneis vel caeruleis punctatis ad basem limbi, tepalis exterioribus 20–24 mm longis, unguibus 5–7 mm, tepalis interioribus trifidis, filamentis ca. 5 mm longis, libris propre apicem, antheris ca. 4 mm longis, ramis styli 4 mm longis, cristis ca. 4 mm longis.

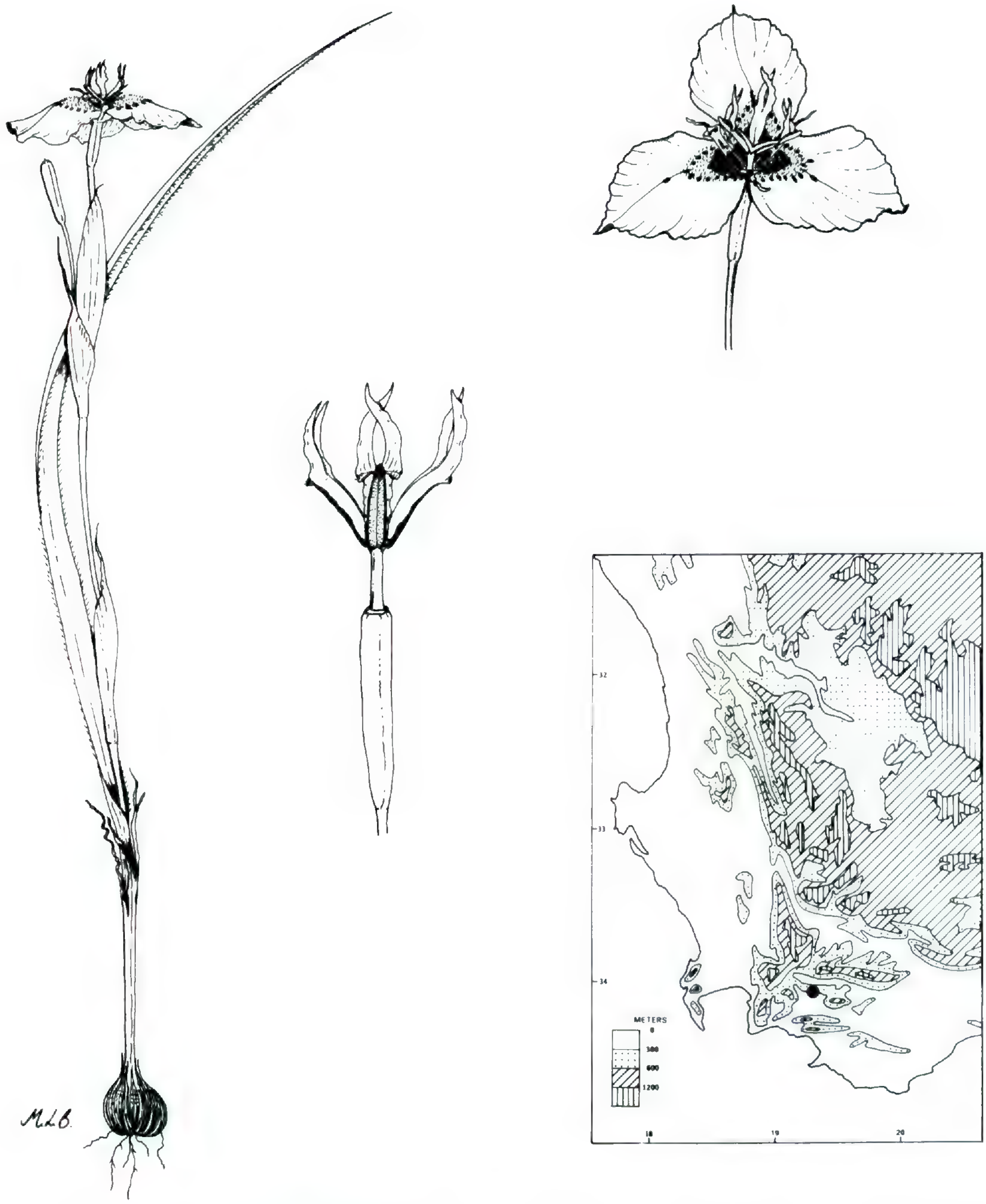

FIGURE 4. Morphology and distribution of *Moraea atropunctata*. Habit ×0.5; flower ×1; detail of ovary, stamens and style branches ×2.

Plants 15–20 cm high. *Corm* 9–12 mm in diameter, tunics of light brown netted fibers. *Cataphyll* often conspicuous and dark brown. *Leaf* solitary, basal, linear, canaliculate, margins ciliate-pubescent, 4–8 mm at widest point, usually erect, about twice as long as stem. *Stem* erect, simple or 1-branched, glabrous, stem bracts 2.5–4 cm long, attenuate, brown above. *Spathes* herbaceous, attenuate, brown above, 4.5–6.5 cm long, outer about half the inner. *Flower* cream to white,

brown on reverse of tepals, spotted dark brown or blue toward base of outer tepal limbs, and nectar guide yellow; *outer tepals* 20–24 mm long, claw 5–7 mm, dark colored and bearded, limb horizontal, 17–25 mm wide; *inner tepals* 9–15 mm long, three-lobed, inner lobe longest, acute, straight or twisted, lateral lobes short, obtuse, yellow, speckled brown, and darker below. *Filaments* ca. 5 mm long, united, free in upper 0.5 mm; *anthers* ca. 4 mm long. Ovary 10–14 mm long; *style* 5 mm, branches as long as anthers, *crests* ca. 4 mm long, orange. *Capsule* oblong, 2.5–3.5 cm long, somewhat inflated, seeds not seen. *Chromosome number* $2n = 12$ (*Goldblatt 5635*).

Flowering time: mid-August–September.

Distribution: known only from a small area of the Eseljacht Mts., N of Caledon, on clay soil.—Fig. 4.

Moraea atropunctata first came to the attention of botanists in 1978 when a bunch of cut specimens was exhibited at the Caledon Wild Flower Show. The following year, specimens again appeared at the Show and Dr. I. Williams obtained several specimens for preservation. He also managed to discover the source of the plants. They were picked by Mrs. G. le Roux, on her farm on the slopes of the Eseljacht Mts. The following year, Mrs. le Roux kindly showed me where the plants grew, and permitted me to make the type collection. The known range of *M. atropunctata* is restricted to a tiny area along a farm road in unploughed, virgin land at the edge of wheatfields. It seems likely that the former range was larger, but *M. atropunctata* may never have extended beyond the limits of the farm where it now occurs.

It is a very unusual species both in flower and vegetative morphology. While it is probably related to *Moraea tricuspidata* and the *M. unguiculata* group in general, it has broad, fairly short leaves with pubescent margins that are unusual in this alliance. Pubescence is unknown in other species of the *M. unguiculata* alliance but common in the related *M. villosa* group of species. The large, inflated capsule is also a characteristic of the *M. villosa* group. The flower, however, is more consistent with the *M. unguiculata* alliance in its dull coloration and three-lobed inner tepals with relatively short central and often somewhat twisted cusp. The chromosome number is $2n = 12$ and the karyotype (Goldblatt, in prep.) is consistent with those described for *M. unguiculata* and its allies.

SOUTH AFRICA: Cape 3414 (Caledon) Vleitjies farm, Caledon dist., Eseljacht Mts., heavy clay soil (AB), *Goldblatt 5635* (K, MO, NBG, PRE, S, US), *Goldblatt 5863* (MO), *Williams 2834* (NBG).

6. Moraea calcicola Goldbl. sp. nov. TYPE: South Africa, Cape, hill tops above Saldanha Bay, *Goldblatt 4118* (MO, holotype, BR, E, K, NBG, PRE, S, US, WAG, isotypes).—FIG. 5.

Planta 30–40 cm alta, tunicis cormi pallidis brunneis, folio unico canaliculato basali, villoso, caule pubescente, simplice vel uniramoso, spathis 5–7 cm longis, flore caeruleo, limbis atrocaeruleis ad basem, tepalis exterioribus 25–35 mm longis unguibus 8–10 mm longis, tepalis interioribus trifidis, filamentis connatis 2–2.8 mm longis in apicem libris, antheris 5.5–6.5 mm longis, ramis styli latis ca. 6 mm longis, cristis ca. 4 mm longis.

Plants slender, 30–40 cm high. *Corm* 9–12 mm in diameter, tunics light brown, reticulate. *Leaf* solitary, basal, linear, canaliculate, exceeding the stem, villous on abaxial surface, 3–5 mm at widest, often bent and trailing. *Stem* erect or

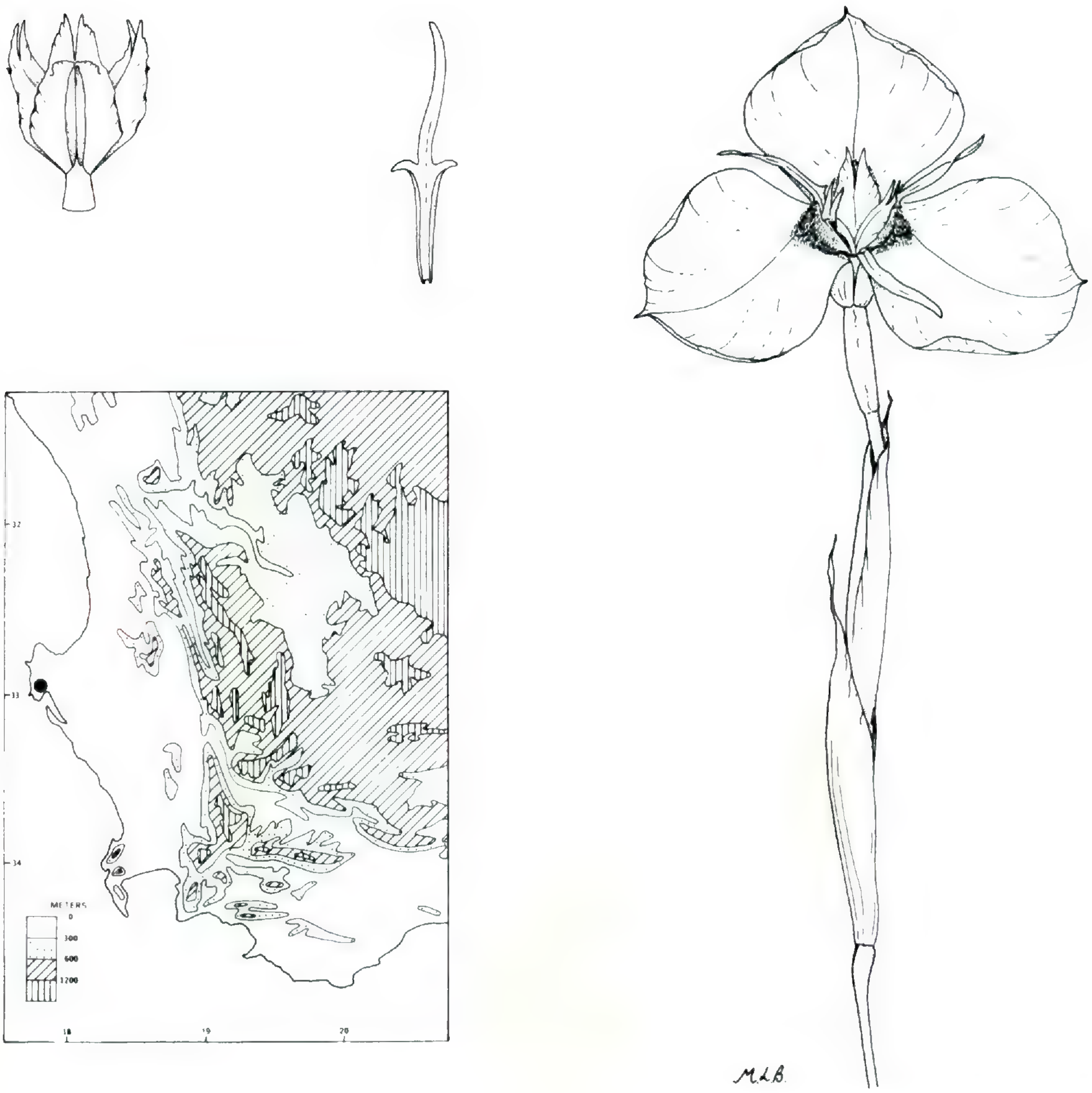

FIGURE 5. Morphology and distribution of *Moraea calcicola*. Flower and spathes ×1; inner tepal ×1; stamens and style branches ×1.5.

inclined, simple or 1-branched, puberulous, stem bracts 5–6 cm long, attenuate and dry above. *Spathes* herbaceous, becoming dry from apex, attenuate, 5–7 cm long, outer 3–5 cm long. *Flower* clear blue, becoming paler with age, faintly scented, nectar guide a small dark blue triangle at base of tepal limb; *outer tepals* 25–35 mm long, limb 15–25 mm long and up to 32 mm wide, spreading horizontally, claw 8–10 mm long, ± erect, heavily bearded with dark blue hairs; *inner tepals* 14–22 mm long, tricuspidate, with long acute central cusp, held horizontally; and short, obtuse, erect lateral lobes. *Filaments* 2–2.8 mm long, free in upper 0.5 mm; *anthers* 5.5–6.5 mm long. Ovary 1–1.5 cm long; *style* 2 mm long, branches inclined, to 6–8 mm long, ca. 6 mm at broadest point, just exceeding anther apex; *crests* ca. 4 mm long, margins broken irregularly. *Capsule* unknown. *Chromosome number* $2n = 12$ (*Goldblatt 4118*).

Flowering time: September.

Distribution: hill tops and slopes above Saldanha Bay, among limestone rocks.—Fig. 5.

Moraea calcicola is related to *Moraea villosa* and its allies, a group loosely known as peacock moraeas. These species are characterized by having large brightly colored and very broad outer tepals, often with conspicuous nectar guides in contrasting pale and dark bands, and tricuspidate inner tepals. Several of the species of the group, including *M. villosa* itself, have puberulous stems and villous leaves; it is to these species that *M. calcicola* is most closely related. *Moraea calcicola* differs from *M. villosa* in its flower color and markings, which are clear blue, with rather inconspicuous nectar guides. Apart from color differences, it is more slender than *M. villosa* and has closer set outer tepals with darkly bearded claws 8(–10) mm long and relatively short filaments 2–3 mm long. *Moraea villosa* has purple, rarely pink, orange or cream colored flowers with large dark nectar guides and contrasting yellow tepal claws 8–12 mm long, and filaments ca. 5 mm long.

The dark colored beard on the outer tepal claws of *Moraea calcicola* is reminiscent of *M. loubseri* (Goldblatt, 1976b), which has outer tepals with a heavy beard covering tepal claws and part of the limb as well. This similarity may indicate a close relationship between thse two species. Both *M. calcicola* and *M. loubseri,* are diploid species, $2n = 12$, and have very restricted ranges along the western Cape coast in the Saldanha Bay district. *Moraea calcicola* occurs on the low hills above the town of Saldanha Bay, and grows among limestone rocks. *Moraea loubseri,* now probably extinct in the wild, is known only from a single granite hill near Langebaan, a short distance to the south of Saldanha Bay. *Moraea villosa* is a much more widespread western Cape species. It occurs in flats and mountain slopes between Piketberg in the north to Gordons Bay in the south, and extends inland to Gydo Pass near Ceres. The several populations of subspecies *villosa* examined cytologically are polyploid, $2n = 24$, while the local subspecies *elandsmontana,* is like *M. calcicola,* diploid, $2n = 12$.

SOUTH AFRICA: Cape 3217 (Vredenburg) hills above Saldanha Bay, among limestone rocks (DD), *Goldblatt 4118* (BR, E, K, MO, NBG, PRE, S, US, WAG).

7. **Moraea villosa** subsp. **elandsmontana** Goldbl. subsp. nov. TYPE: South Africa, Cape, S of Gouda at foot of Elandskloof Mts. on farm Elandsberg, *Goldblatt 6202* (MO, holotype, K, NBG, PRE, S, isotypes).—FIG. 6.

Hic differt a subspecies villosa colore aurantiaco vel albo, macula lunari atrocaerulea in base limbis tepalorum exteriorum, tepalis exterioribus ascendentibus et numero diploideo chromosomatum $2n = 12$.

Plants like *Moraea villosa* in vegetative characteristics, but stem usually simple. *Flower* bright orange with navy blue nectar guide at base of outer tepal limb; *outer tepals* 28–31 mm long, claw 8–11 mm, limb ascending, not horizontal, margins curving upward; inner tepals also orange, ca. 21 mm long. *Filaments* 4–5 mm long, free in upper 1 mm; *anthers* ca. 7 mm long. Ovary 7–10 mm long; *style branches* ca. 6 mm long, orange or white, *crests* ca. 5 mm. *Chromosome number* $2n = 12$ (*Goldblatt 6202*).

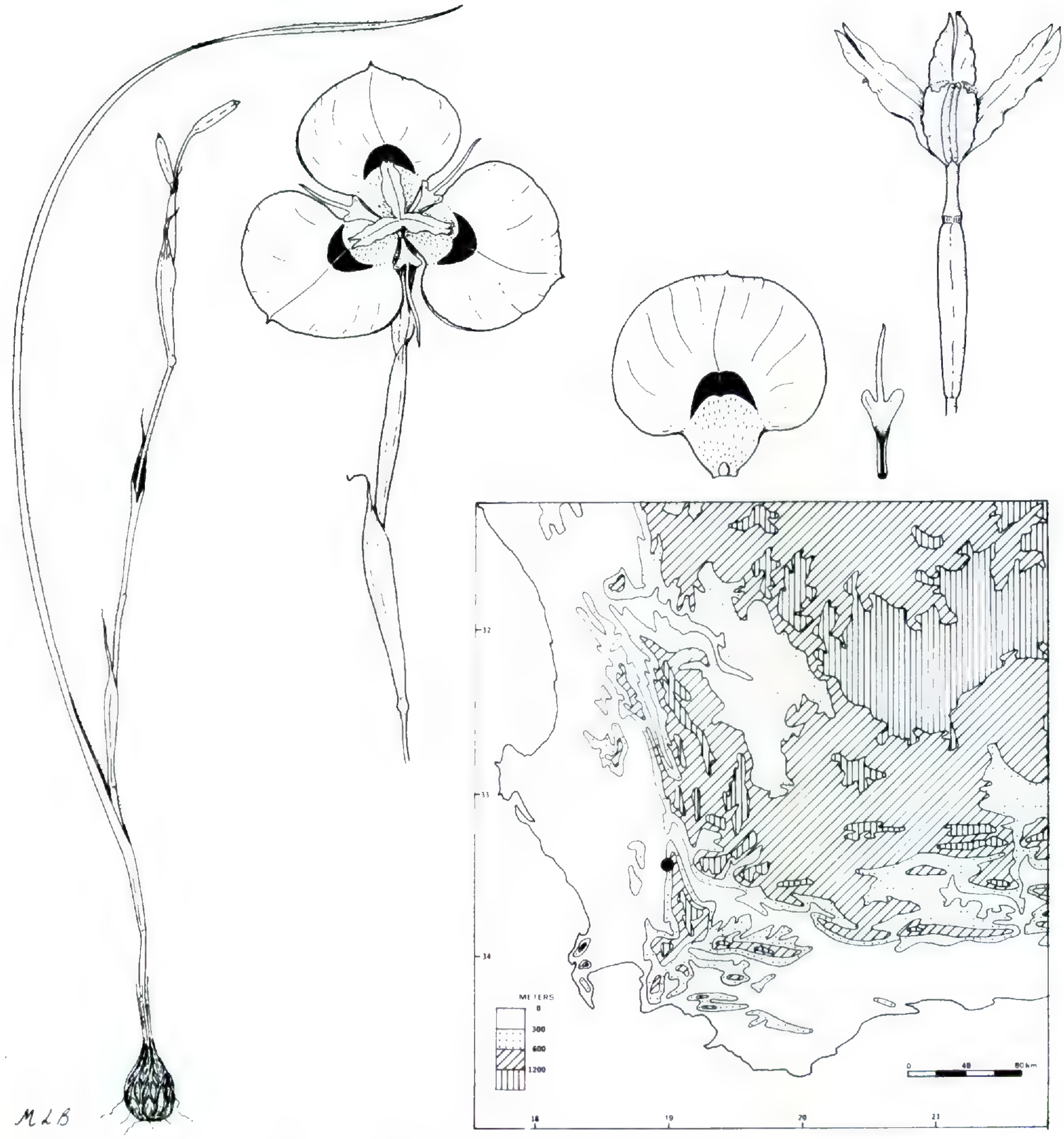

FIGURE 6. Morphology and distribution of *Moraea villosa* subsp. *elandsmontana*. Habit ×0.5; flower, spathes and tepals ×1; detail of ovary, stamens, and style branches ×1.5.

Flowering time: September.

Distribution: local, at the foot of the Elandskloof Mts., in very stony sandstone soil in fynbos.—Fig. 6.

Moraea villosa is one of the more common and widespread of the group of species known as peacock moraeas for the large, conspicuous eye-like nectar guides on very broad outer tepals. It ranges from the Piketberg Mts. and upper Olifants River Valley in the north to Gordons Bay in the South, with extensions inland through the Tulbagh Valley to Ceres and Gydo Pass. It is believed to be tetraploid, $2n = 24$ throughout its range, as is the related *M. tulbaghensis*.

The subspecies *elandsmontana* of *M. villosa* described here has most of the

attributes of *M. villosa,* but it differs sharply in its bright orange flower color. The flowers are also a little unusual for *M. villosa* in having a relatively small, dark nectar guide, and in having the outer tepals ascending and with upcurved margins. More often the tepals of *M. villosa* are flat and horizontal to slightly reflexed, although forms with slightly ascending tepals do occur. The flowers of *M. villosa* are usually shades of blue or purple, or occasionally whitish or even pink.

It is however, the diploid chromosome number of $2n = 12$, in contrast to the tetraploid level $2n = 24$ of other populations of *Moraea villosa,* that sets subsp. *elandsmontana* apart rather than its unusual flower color and minor tepal differences, which alone would not merit taxonmic recognition. Subspecies *elandsmontana* is known only from Elandsberg farm at the foot of the Elandskloof Mts. south of Gouda. It is locally common on gently sloping rocky sandstone ground. Presently it is under protection because it grows in a portion of Elandsberg farm set aside by the owner Dale Parker as a nature reserve. The typical subspecies of *M. villosa* also occurs on Elandsberg, not far from the populations of subspecies *elandsmontana* but in a different habitat, on richer and deep sandy to clayish soils.

SOUTH AFRICA: Cape 3314 (Worcester) foot of Elandskloof Mts. on farm Elandsberg, S of Gouda (AC), *Goldblatt 5854* (MO), *6202* (K, MO, NBG, PRE, S), *Burgers 1233* (MO); Elandsberg Nature Reserve, foot of Elandskloof Mts., 4 km N of Bosplaas, *Burghers 2802* (STE).

SUBGENUS *GRANDIFLORA*

8. Moraea robusta (Goldbl.) Goldbl. comb. nov.

Moraea galpinii subsp. *robusta* Goldbl., Ann. Missouri Bot. Gard. 60:248. 1973. TYPE: South Africa, Natal, Naauwhoek, Utrecht distr. *Devenish 109* (PRE, holotype).

A recent collection and photographs of this plant from the type locality made by O. M. Hilliard and B. L. Burtt, *9153*, have provided new information about its morphology and relationships. In 1973 in my revision of *Moraea* in the summer rainfall areas of southern Africa (Goldblatt, 1973) I treated it as a subspecies of the better known *M. galpinii*. This is a very short species 15–30 cm tall, having moderate-sized, bright yellow flowers with erect inner tepals (Obermeyer, 1970). Its leaves are evidently terete but actually are narrow with margins tightly inrolled and narrow adaxial groove. The leaf is very long, but often dying back, or absent, on flowering plants, but the new season's leaves may be present in a clump of plants, and, if so, are often quite short. *Moraea galpinii* blooms before the onset of spring rains, from late July to October, and it grows in open grassland.

The subspecies *robusta,* when described, was believed to be similar in most respects, but with larger flowers of pale yellow to white color, wider leaves with less tightly inrolled margins, and possibly later blooming.

The specimens collected by Hilliard and Burtt in early November confirm my previous observations on larger size and paler flower color, but the photographs of the flower indicate that the inner tepals are flaccid and spreading rather than being held stiffly erect. This difference is important because all other species of subgenus *Grandiflora* have erect inner tepals, and it now seems desirable to raise subspecies *robusta* to species rank.

Moraea robusta shares with *M. galpinii* the very characteristic mass of dark fibers accumulated round the base of the plants and it seems likely that the two species are closely related despite floral differences. The usual flowering time of *M. robusta* is mid-October to November but a sheet collected by Thode, *A363*, has the vague date "Aug., Sept. 1924," which, if correct, suggests much earlier blooming in some populations. The amended description is as follows:

Plants 30–40 cm high. *Corm* covered by dark densely matted fibers. *Leaf* 4–10 mm wide, margins incurved, exceeding stem, and often dead above. *Stem* with 3 overlapping stem bracts. *Spathes* 10–11 cm long, outer ±⅔ the length of inner. *Flower* pale yellow to white, tepals spreading horizontally when fully open; *outer tepals* 5.5–6.5 cm long, limb 4 cm long and to 2.6 cm wide; inner tepals 5.5–5.7 cm long. *Filaments* 10–11 mm long, free in upper half, *anthers* ca. 10 mm long. Ovary ca. 15 mm, *style branches* 15 mm, *crests* ±15 mm.

Flowering time: (?Aug.–Sept.) Oct.–Nov.

Distribution: high altitude grassland, SE Transvaal, N Natal, E Orange Free State, and Transkei.

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CORM MORPHOLOGY IN *HESPERANTHA* (IRIDACEAE, IXIOIDEAE) AND A PROPOSED INFRAGENERIC TAXONOMY[1]

PETER GOLDBLATT[2]

ABSTRACT

The corm tunics of species of *Hesperantha* vary to a remarkable extent in this African genus in which other morphological characteristics provide little information for classification above the species level. The presumed basic corm type is globose and distinctly asymmetric and has concentric tunics. Globose corms with imbricate tunics, distinctly notched below are believed to be derived while the most specialized are flat-sided and triangular to campanulate in outline, with imbricate tunics, either more or less unbroken below, or notched into segments and often spiny or toothed below. This variation appears to form a coherent pattern and is emphasized in an infrageneric classification in which other taxonomically useful characters are taken into account. Four sections are recognized. Species with concentric corm tunics are assigned to section *Concentrica*; those with globose corms and imbricate tunics are assigned mostly to section *Imbricata*; while most of those with symmetric, campanulate to triangular, flat sided corms with imbricate tunics are assigned to section *Hesperantha*. A distinctive group with bracts having margins partly united around the stem, and either globose or campanulate corms with imbricate tunics are assigned to section *Radiata*. A brief survey of the distribution and distinctive species of each section is outlined following the formal taxonomic descriptions.

INTRODUCTION

Hesperantha is a genus of some 55 species of Iridaceae, Ixioideae, distributed widely in sub-Saharan Africa. The genus consists of small to medium-sized corm-bearing plants, often with white, or pale-colored flowers and a characteristic stigma that divides into three long branches at the mouth of a relatively long perianth tube. Species are concentrated in the winter rainfall region of southern Africa, where some 34 species occur in the southwestern Cape, the adjacent western Karoo and Namaqualand. There is a secondary center in the higher mountains of eastern southern Africa, especially the Drakensberg of Natal and Lesotho. The number of species falls sharply northward through the Transvaal and Zimbabwe with only one species extending into the mountains of East Africa, Ethiopia and Cameroon. *Hesperantha* is currently being studied by O. M. Hilliard & B. L. Burtt (1979:302–304, and in prep.) in the eastern part of its range in the Drakensberg of Southern Africa, and by myself in the Cape winter rainfall area.

A cormous rootstock is a characteristic feature of several monocot families particularly those of Liliaceous affinities, notably Tecophilaeaceae, Colchicaceae, and Iridaceae (Dahlgren & Clifford, 1982). In Iridaceae two different corm types occur (Goldblatt, 1976:670; de Vos, 1977), one in Iridoideae and the other in Ixioideae, to which *Hesperantha* belongs. In Ixioideae variation in corm morphology is considerable, involving shape, size, number of nodes and nature of

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ANN. MISSOURI BOT. GARD. 69: 370–378. 1982.

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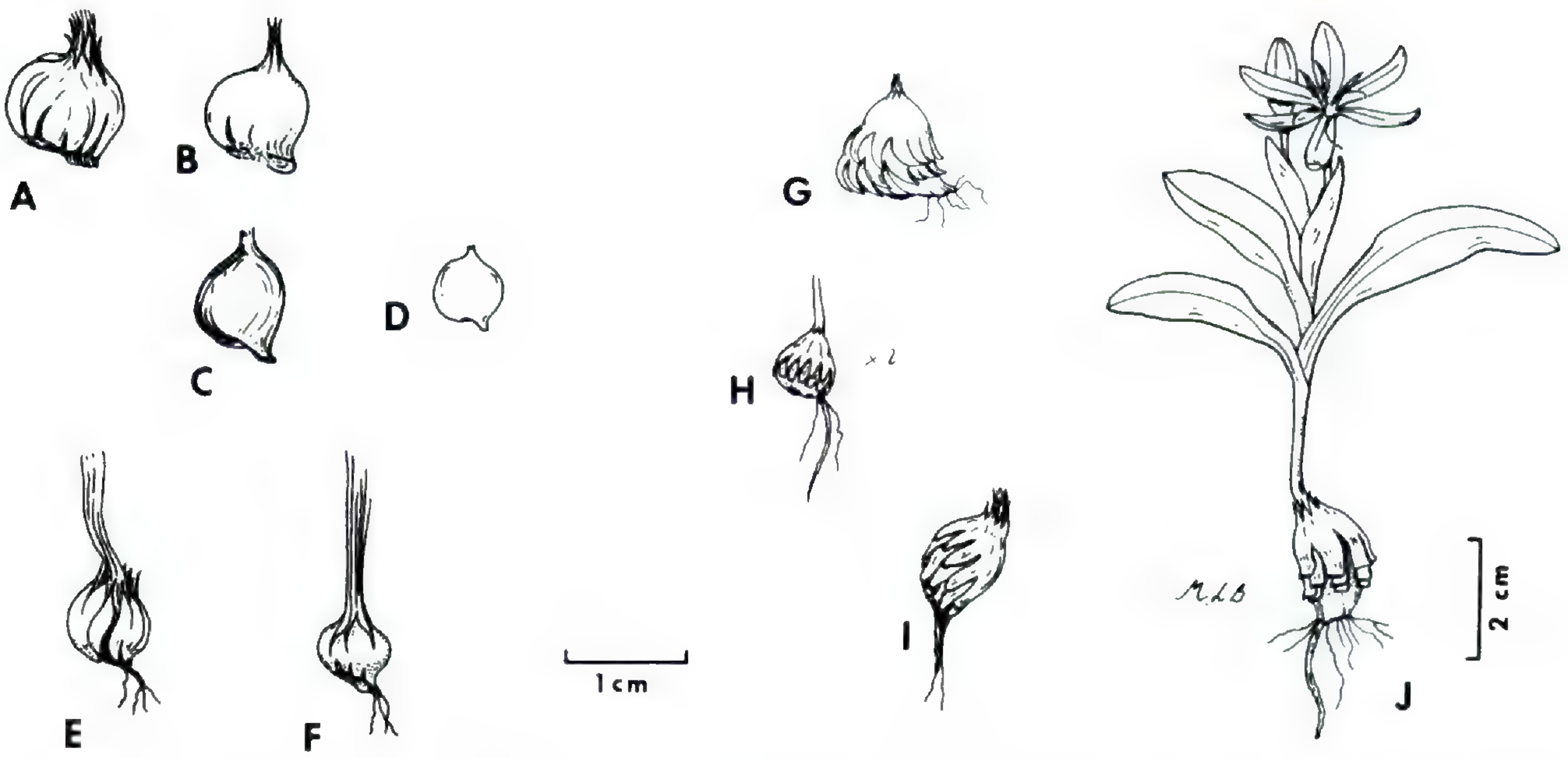

FIGURE 1. Corm morphology of *Hesperantha* sections *Concentrica* (A–F) and *Imbricata* (G–J): A–D. *H. pilosa* with tunic layers progressively removed and the naked corm (D); E. *H. rivulicola*; F. *H. fibrosa*; G. *H. vaginata*; H. *H. bachmannii*; I. *H. pallescens* (bulbils removed); J. *H. humilis* (all more or less life size except J, ×0.5).

the covering layers, which are called tunics. The tunics are derived from specialized cataphylls or the lower parts of the basally sheathing cataphylls or produced leaves and they may be considerably modified and elaborated in some genera. They vary from coarsely to finely fibrous and reticulate to thick and woody in texture. A general discussion of the corms found in Iridaceae is given by Lewis (1954).

In *Hesperantha* corm morphology varies to a remarkable extent within the genus, particularly in the species of the winter rainfall area of southern Africa and this has until now been inadequately documented. The morphology of the corm and corm tunics is described in detail below, followed by a discussion of other important morphological characters. A classification in which corm characteristics are emphasized is presented in the taxonomic part of the paper. My knowledge of the species of eastern southern Africa is limited so that the scheme is based largely on the winter rainfall area species. I hope nevertheless that the classification will prove applicable to the entire genus. A preliminary examination of species outside the winter rainfall area suggests that they can be accommodated in the classification outlined below, although creation of further sections may prove necessary.

CORM MORPHOLOGY

The morphology of the living tissue of the corm of all species of *Hesperantha* is similar except for slight variation in size and shape. The corm is fundamentally asymmetric. Although globose to depressed-globose in general shape, a small projecting ridge is always present at one end of the corm (Fig. 1D, Fig. 2F) and it is from this point only that the roots are produced.

The corm is always covered by specialized layers of tunics and in *Hesperantha* these are usually woody in texture and a single layer is produced annually. The

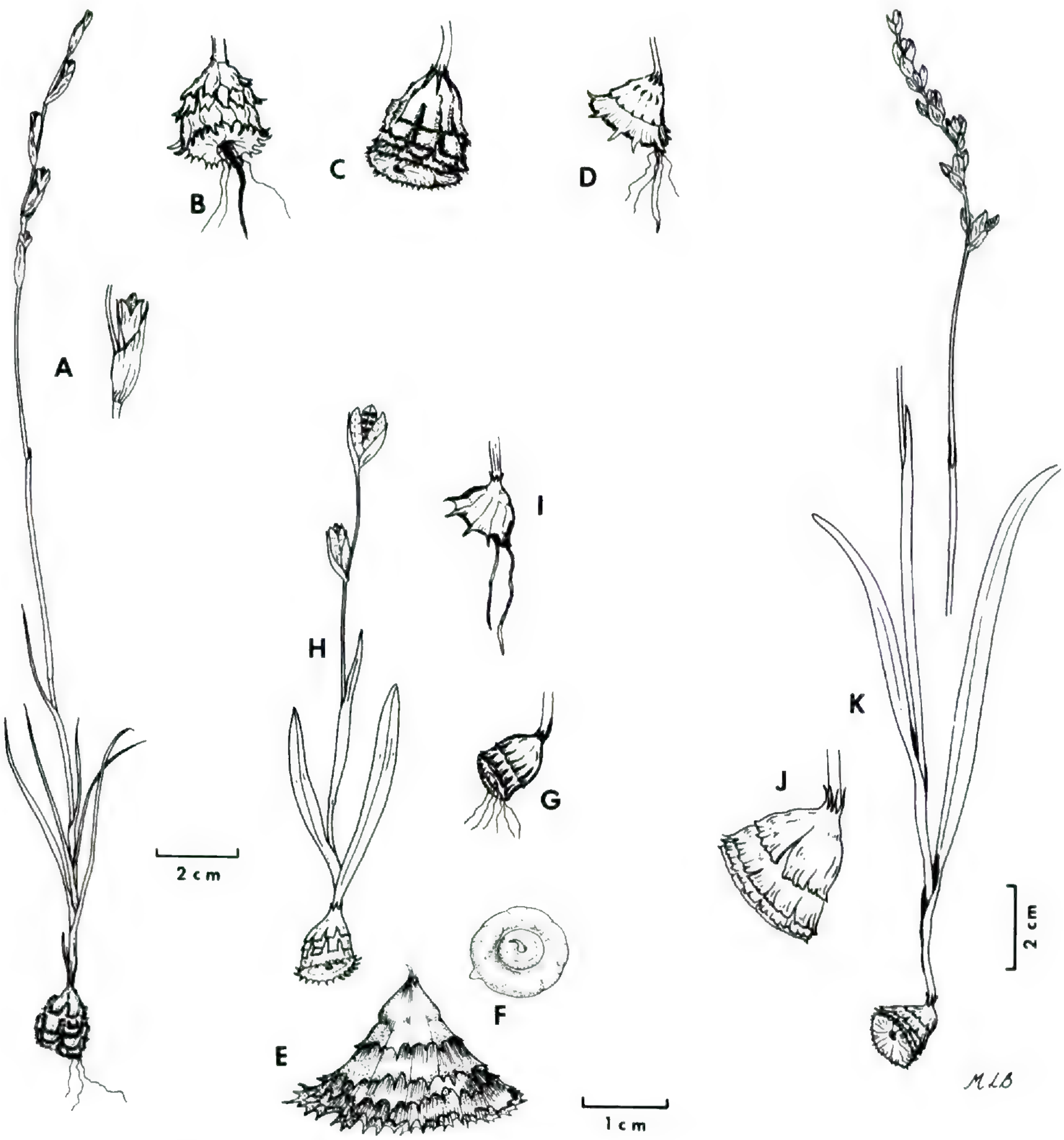

FIGURE 2. Corm morphology of *Hesperantha* sections *Radiata* (A–D) and *Hesperantha* (E–J): A. *H. radiata*, with part of spike enlarged to show sheathing bract; B. *H. radiata*; C. *H. muirii*; D. *H. marlothii*; E. *H. falcata*; F. *H. falcata*, naked corm with tunics removed; G. *H. falcata*; H. *H. cedarmontana*; I. *H. luticola*; J–K. *H. spicata* (all more or less life size except A, H and K, ×0.5).

appearance of the tunics and the way in which they accumulate seems to be the single most taxonomically useful character in the genus above the species level.

The simplest tunic type, and possibly the ancestral condition, since it is also found in species of the related genus *Geissorhiza* (Foster, 1941), is one in which the corm tunics are arranged in concentric layers (Fig. 1A, E, F). In this type the corms are usually more or less globose, with one side flattened below and the flat part extending downward for a short distance. This asymmetry reflects the internal morphology. The tunic layers are usually firm and brittle, but occasionally, especially in high mountain species (e.g. *H. montigena* Goldbl. ined.) they may be papery. Newly formed tunic layers are enclosed by the outer ones

and as successive layers accumulate, the older, outermost ones fragment vertically above and below into regular or more or less irregular-sized pieces (Fig. 1A, E, F). Concentric corm tunics are found in many species that extend throughout the range of the genus and grow in a variety of habitats from moist, well watered situations to arid sites.

A second corm type has imbricate tunics and this is presumed to be the derived condition. Here, the outer layers are displaced upward as new tunic layers are produced annually. The outer layers are typically notched below at regular intervals so that that the lower part of each layer is divided into even-sized segments. The mid-to-upper portion remains unbroken but may become shallowly notched above (Fig. 1G–J, Fig. 2).

Species with tunics of this type may either have globose but asymmetric corms (Fig. 1G, H, I) with one side flattened below and produced downward, or symmetric corms, triangular to campanulate in outline (Fig. 2) with one side completely flat. This type of corm is usually called flat-based although in the ground the flat side is oriented vertically or inclined, and is only basal (i.e. horizontal) in plants growing in shallow soil over rock.

In plants with imbricate corms, the lower margins of the tunic layers may be somewhat fringed (e.g. *H. radiata* (Jacq.) Ker, *H. muirii* (L. Bol.) Lewis; Fig. 2A, C), toothed (e.g. *H. radiata, H. falcata* (L. f.) Ker; Fig. 2B, E) or even long-spined (e.g. *H. marlothii* Foster, *H. luticola* Goldbl. ined.; Fig. 2D, I), particularly in species with symmetric, flat-sided corms. In some species with flat-sided corms the outer layers do not split into segments but remain almost entire or lightly fringed to toothed, notably in *H. spicata* (Burm. f.) N.E. Br. (Fig. 2J, K).

Some variation is evident in a few species, notably *Hesperantha radiata* (Fig. 2A, B), in which the tunic margins may be lightly fringed to toothed. In *H. falcata* the corms range from triangular to campanulate in outline (Fig. 2E, G) and the lower tunic margins may be unbroken or variously serrate to toothed.

The distribution of various corm types follows a coherent pattern. Obviously allied species have similar corms, and apparently distantly related species usually have different corms. In this light it has seemed reasonable to regard corm morphology as a very reliable indication of taxonomic relationship. An infrageneric taxonomy in which the corm characteristics are strongly emphasized is proposed in the second part of this paper.

Other Morphological Characteristics

habit, leaf and stem

Most species of *Hesperantha* are small to moderate-sized herbs with simple to few branched, aerial stems. One modification that stands out is suppression of the stem and consequent acaulescent habit. Accompanying the stem reduction are flowers with long perianth tubes and large, leaf like floral bracts. This habit occurs in *Hesperantha latifolia* (Klatt) de Vos, a Namaqualand species; in four western Karoo species, *H. humilis* Baker, *H. flava* Lewis and *H. hantamensis* Schltr. ex Foster, and the apparently unrelated *H. luticola*; as well as in the Drakensberg species *H. crocopsis* Hilliard & Burtt. This growth form seems to have arisen independently at least four times, judging from lack of correlation

with other characters. *Hesperantha humilis* does appear closely allied to two other species with these features, *H. hantamensis* and *H. flava,* but it does not seem worthwhile to recognize this alliance in a formal taxonomic way because this overemphasizes the significance of these characters and obscures their close relationship with several caulescent species of the western Karoo.

There is little else of broad taxonomic importance in the vegetative characters. Unusual leaf modifications occur in a few species, e.g. thickened margins in *H. fibrosa* Baker, pubescence in *H. pilosa* (L. f.) Ker, terete form in *H. juncea* Goldbl. ined., but none of these characteristics are of more than specific significance. Often one leaf is modified to sheath the lower part of the stem, while a second one may become bract-like and without a free apex. These trends seem to be repeated in several lines, and do not appear to constitute a character of much value above species level.

FLOWER AND FLORAL BRACTS

Floral variation in *Hesperantha* is fairly limited. All but a few species have similar, small, actinomorphic flowers, with moderately long, straight perianth tubes and subequal, spreading tepals. White to cream colored flowers predominate in the genus, but pink is the most common color in species in eastern southern Africa and the tropics (B. L. Burtt, pers. comm.). White and cream flowers are evening blooming, and brightly colored ones generally day blooming. In the winter rainfall area there are species with pink, purple, blue, or yellow and often large flowers and these seem to have evolved repeatedly from ancestors with small white flowers. Thus flower color appears to have limited taxonomic value.

A curved perianth tube is present in several species: notably in *Hesperantha radiata* and its relatives; in *H. bachmannii* and *H. bulbifera*; and in *H. grandiflora*. Judging from associated morphological features, these three groups are unrelated. *Hesperantha grandiflora* seems unique in having truly declinate stamens and is zygomorphic. In other species with a curved perianth tube the stamens tend to fall together as they hang downward, thus appearing more or less unilateral. The stamens are included in the perianth tube in the two unrelated species *H. elsiae* Goldbl. ined. and *H. cedarmontana* Goldbl. ined.

Floral bracts are always herbaceous, usually of moderate size, and about as long as the perianth tube. The bracts are noticeably well developed in the very long-tubed species such as *Hesperantha grandiflora, H. huttonii,* and some other eastern species and also in the acaulescent species of the western Karoo like *H. humilis, H. flava,* and *H. luticola*. The outer bracts of *H. radiata* and its allies are distinctive in having a lower tubular portion encircling the stem, sometimes for as much as two-thirds of their length (*H. radiata*) but barely so in *H. marlothii,* which nevertheless seems allied to the group. These unusual bracts seem to unite a group of species that have other shared features such as curved perianth tubes and characteristically short narrow leaves. This apparently natural alliance includes the widely distributed *H. radiata–H. tysonii* complex and several local southwestern Cape endemics, as well as the Transvaal–Zimbabwe–Malawi *H. longicollis*. It seems useful to give taxonomic recognition here to the alliance, all species of which have imbricate corm tunics.

Cytology

Basic chromosome number in *Hesperantha* is $x = 13$ (Goldblatt, 1971, and in prep.). Some 25 species have so far been counted, covering the entire range of the genus, and no variation in numbers has been found, except for the presence of B chromosomes in *H. luticola*.

Subgeneric Classification

I have decided on sectional rank for each major infrageneric grouping even though the concentric versus imbricate tunic type seems of more fundamental significance than the subtypes of imbricate tunic (and hence perhaps deserving of higher ranking). This is because of the difficulty in assigning certain species to tunic type (owing to distortion by accumulation of old tunics, to soil conditions, or to apparent intermediacy of the corm for this character).

Although corm morphology has been emphasized, all features of the plant have been taken into consideration. The following infrageneric system is proposed. Those species with concentric corm tunics are assigned to what may be considered the least specialized section, *Concentrica*. Species with imbricate tunics have been divided among three sections. Section *Imbricata* includes species with more or less globose, asymmetric corms and bracts with free margins.

Species with bracts having margins partly united around the stem seem to form a natural alliance and are assigned to section *Radiata*. The corm tunics vary in this section (Fig. 2A–D), but the globose corm with tunics notched below is seen as basic here, with symmetric, flat-sided corms being derived.

A fourth section, *Hesperantha*, appears to constitute a natural alliance amongst the species with imbricate corm tunics and is characterized by having symmetric, flat-sided corms, campanulate to triangular in outline. This corm type is a modification of the asymmetric corm of section *Imbricata*, in which the small flattened area at one end of the corm has become enlarged into a conspicuous broad flat side.

HISTORICAL NOTE

The only significant systematic treatments of *Hesperantha* that deal with substantial numbers of species are Baker's revisions in *Handbook of the Irideae* (1892) and in *Flora Capensis* (1896). In neither study was any subgeneric classification established. The main key characters were presence of a straight or curved perianth tube and flower and leaf size. These characters separated species adequately but did not establish any natural groupings. Foster (1948), the only other systematist to have worked extensively on the genus, produced a preliminary study of *Hesperantha* that included corrections to nomenclature and many new species, but this work was not by any means a revision, and no infrageneric classification was presented. Thus the system presented here is essentially new and not founded on any earlier study.

TAXONOMIC TREATMENT

1. **Hesperantha** sect. **Concentrica** Goldbl. sect. nov. TYPE: *H. pilosa* (Thunb.) Ker.

Cormus globosus, ± symmetricus vel asymmetricus, infra ± complanatus, tunicis concentricis, saepe supra subspinosis, floribus actinomorphis vel zygomorphis, albis, rubrescentibus in reversis tepalae exterioris, vel caeruleis, carneis, purpureis, raro flavis, tubo usitato bracteae aequali, in aliquot speciebus perlongo.

Corm ± symmetric to asymmetric, with one side flattened below, the flat side often extending downward for some distance, tunics concentric, outer layers completely enclosing inner, fragmenting irregularly into unequal sections, often drawn into points above. Flowers actinomorphic rarely zygomorphic, whitish, blue, pink, or purple, occasionally yellow, often small, tube well extended from bracts in a few species. Leaves pilose in *H. pilosa* or ciliate in *H. ciliolata*, margins thickened in *H. fibrosa* and occasionally in *H. pilosa* and other species.

Distribution: widespread, southwest Cape to Ethiopia and Cameroon.

Type species: *H. pilosa* (Thunb.) Ker Species: ca. 25

Section *Concentrica* comprising about 25 species, is the largest and most widespread section, ranging from the southwestern Cape to Ethiopia and Cameroon. It has radiated extensively in the southern African Drakensberg, and in the southwestern Cape and western Karoo where some 11 species occur. An evolutionary trend is evident in the reduction in number of leaves to three, one of which partly sheaths the stem. A specialized bract leaf is present on the stems of several species, this sometimes membranous and scale-like. *Hesperantha pilosa* is the only pubescent species in the genus, and *H. ciliolata* is the only one with ciliate leaves. Unusual corm tunics occur in *H. fibrosa* in which the upper part of the tunic is drawn into very long, persistent fibers. In several Drakensberg species and the tropical African *H. alpina* the tunic layers may be papery in texture, rather than brittle and woody. A similar condition is present in *H. montigena* of the SW Cape Mts.

2. Hesperantha sect. **Imbricata** Goldbl. sect. nov. TYPE: *H. humilis* Baker.

Cormus asymmetricus, ± globosus, tunicis imbricatis, infra in segmentis aequalibus incisis, floribus actinomorphis, albis, carneis, luteis, raro maculis atrocoloris, tubo perianthii recto vel curvato in *H. bachmannii* et *H. bulbifera*, habitu caulescenti vel acaulescenti.

Corm ± asymmetric, with one side flattened, and sometimes extending downward for a short distance, imbricate, outer layers overlapping inner above only, usually fragmenting regularly below into even-sized sections, sometimes drawn into points above. Flowers actinomorphic, white, pink, purple, yellow, sometimes with dark contrasting markings, small to large, tube well exserted from bracts in several species, perianth tube curved in *H. bachmannii* Baker and *H. bulbifera* Baker. Plants caulescent or acaulescent, and then with large bracts.

Distribution: centered in western Southern Africa, mainly in arid areas. Namaqualand to Transvaal.

Type species: H. humilis Baker Species: 12

Section *Imbricata*, comprising some 12 species, is centered in the western Karoo, but in fact extends from northern Namaqualand through the Karoo to the Transvaal. The acaulescent habit is developed in three species, *H. humilis* and *H. hantamensis* of the western Karoo, and *H. flava*, which is known from northern Namaqualand and the Laingsburg district of the Karoo. Two species have a

curved perianth tube, the widespread *H. bachmannii,* and *H. bulbifera,* which occurs in the eastern Cape and at isolated montane sites in the Transvaal. Local endemics include the long-tubed *H. pallescens* Goldbl. ined. from the western Cape and *H. oligantha* Diels and *H. purpurea* Goldbl. ined. from the Calvinia district. The most striking species is *H. vaginata,* which has deep yellow flowers with contrasting dark brown markings.

3. Hesperantha sect. **Radiata** Goldbl. sect. nov. TYPE: *H. radiata* (Jacq.) Ker.

Cormus ± globosus et asymmetricus, vel campanulatus et symmetricus, tunicis infra serratis spinosis vel ciliatis, vel in segmentis aequalibus incisis, marginibus bractearum in parte inferioribus connatis vel ± libris, floribus ± actinomorphis sed tubo perianthii curvato, usitatis pallidis, vel carneis.

Corm either ± asymmetric with one side flattened below or symmetric and campanulate in outline, tunics imbricate, outer covering inner only above, unbroken, or notched regularly below into sections, these sometimes ± ciliate-edged, occasionally lower margins of layers serrate to spiny. Outer bract margins usually united below around the axis, sometimes for over half their length. Flowers ± actinomorphic, but usually with curved perianth tube (straight in *H. juncifolia* Goldbl. ined. and barely curved in *H. brevifolia* Goldbl. ined.) and pendulous, unilateral anthers, white-cream, or pale to deep pink, tube well exerted from bracts in some species.

Distribution: widespread in southern Africa, Namaqualand to Malawi.

Type species: *H. radiata* (Jacq.) Ker Species: 7–9

Section *Radiata* comprises a close knit group of seven to nine species centered around the *H. radiata–H. tysonii* complex. This complex extends from Namaqualand through the southwestern Cape and Karoo into eastern southern Africa as far as Swaziland. Corm tunics vary to an unusual extent even within *H. radiata* sensu stricto, but the characteristic bracts usually with united margins and several, small leaves unite the section. There are several local endemics in the southwestern Cape including the terete-leafed *H. juncifolia* from Bredasdorp coast and *H. elsiae* from the Cedarberg, which has included stamens and style branches. *Hesperantha marlothii,* centered in the Roggeveld, has flat-sided corms with spiny margins and it, as well the SW Cape *H. brevifolia* have bracts in which the margins are barely fused. Section *Radiata* extends into Botswana, Zimbabwe, and Malawi where the long tubed *H. longicollis* Baker occurs in wet sites on the highveld and in mountain areas. *Hesperantha ballii* Wild is a dwarf species of the Chimanimani Mts. of the Zimbabwe–Mozambique border.

4. Hesperantha sect. **Hesperantha**. TYPE: *H. falcata* (L. f.) Ker.

Corm ± symmetric, with a flat base, campanulate to triangular in outline, tunics imbricate, outer covering inner above only, lower margins entire, or serrate or drawn into spines, sometimes notched below into ± even-sized sections. Flower actinomorphic, usually whitish yellow, or pink to purplish, occasionally with darker markings (in *H. luticola*); tube barely to well exserted from bracts; anthers and style branches included in perianth tube in *H. cedarmontana*. Plants acaulescent in *H. luticola,* and usually so in *H. latifolia*.

Distribution: Restricted to the winter rainfall area, southern Cape to Peninsula and north to Richtersveld.

Type species: *H. falcata* (L.f.) Ker Species: 7

Section *Hesperantha*, comprising some seven species, is restricted to the winter rainfall areas of the southwestern Cape, Namaqualand, and the western Karoo. All species have flat-sided, campanulate, to triangular corms often with toothed or spiny margins. Two species, *H. latifolia* and *H. luticola*, are acaulescent and grow in seasonally moist sites such as rock pools and stream edges. Both have long perianth tubes. Other species have fairly small, relatively short-tubed flowers but *H. cedarmontana* is unusual in having included stamens and the very short style and style branches enclosed in the perianth tube. *Hesperantha spicata* and the very localized *H. saldanhae* Goldbl. ined. have an unusually large number of very small flowers per spike. *Hesperantha spicata* subsp. *spicata* often has leaves with undulate margins, while subsp. *fistulosa* has hollow, terete leaves. *Hesperantha falcata* is the only widespread species, and is very variable. Its flowers may be white or occasionally yellow or cream.

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NOTES ON *GEISSORHIZA* (IRIDACEAE): THE SPECIES IN MADAGASCAR[1]

PETER GOLDBLATT[2]

ABSTRACT

The two Madagascar species regarded as belonging to the southern African genus *Geissorhiza*, *G. bojeri* and *G. ambongensis* are shown to have characteristics incompatible with this genus. *Geissorhiza bojeri* accords well with *Gladiolus* and is transferred here as *Gladiolus bojeri* (Baker) Goldbl. *Geissorhiza ambongensis* is not sufficiently well known to allow generic placement at this time but is excluded from *Geissorhiza*.

Geissorhiza is a large genus of southern African Iridaceae subfamily Ixioideae. In the only complete modern treatment of the genus, Foster (1941) recognized 55 species in two subgenera. Subgenus *Geissorhiza* has 51 species, all from the Cape Flora Region and surrounding areas, and subgenus *Ixiopsis* has only four, three of which occur in the Cape Region and the fourth, *G. bojeri* Baker in Madagascar. The second Madagascar *Geissorhiza*, *G. ambongensis*, described in 1939 (Perrier, 1939), was treated by Foster among his doubtful and unknown species. Foster saw no specimens, but commented that from the description, it seemed close to *G. bojeri*, but distinct. Both species were placed in *Geissorhiza* in the Flore de Madagascar (Perrier, 1946). I am at present revising *Geissorhiza* and it has become clear to me during this study that the two Madagascar species do not belong in *Geissorhiza* at all.

THE MADAGASCAR SPECIES OF "*GEISSORHIZA*"

1. *Geissorhiza bojeri*. The earlier of the two Madagascar *Geissorhiza* species, *G. bojeri* was described in 1876 by J. G. Baker, based on collections by Bojer and Hilsenberg from the mountains of central Madagascar. Since then the species has been collected repeatedly and is evidently common on the central plateau in grassland and rocky situations. *Geissorhiza bojeri* is a slender plant, variable in height from 15 to 35 cm, with two linear, equitant basal leaves, and one to three more, smaller, cauline, partly sheathing leaves, the uppermost often bract-like. The small corms have tunics of fine reticulate fibres, the character that Baker used to distinguish subgenus *Ixiopsis*, of which *G. bojeri* is the type species. The bracts are herbaceous and quite short; and the yellow flower is small, short tubed, and apparently actinomorphic, with lanceolate tepals. The fruits are unusual in being long and slender and the seeds have an entire, membranous wing. The seeds match exactly those of *Gladiolus*, and the fruits are similar to fruits of some *Gladiolus* species, although more slender than any other species known to me.

The significant taxonomic characters are the fibrous corm tunics, apparently actinomorphic flower, long capsule, and winged seeds and only one of these, the actinomorphic flower, corresponds with *Geissorhiza* as it is currently understood.

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In *Geissorhiza* the corm tunics of most species are woody and consist of unbroken, or irregularly fragmented layers, although soft tunics are known in a few species, and *G. hesperanthoides,* and two more undescribed species have fibrous tunics. Seeds of all *Geissorhiza* species are irregularly angular and lack a wing, and the capsules are typically small and rotund. Flowers of *Geissorhiza* species are either completely actinomorphic or have declinate stamens and style.

Recently I was shown photographs of *Geissorhiza bojeri* taken in the wild by T. B. Croat in Madagascar. The flower is quite different in appearance from the dried state. It is not actinomorphic, but medianly zygomorphic, with a hooded, horizontal upper tepal under which arch the unilateral stamens and contiguous anthers. The lower three tepals are deeply grooved and each has a transverse band of purple across the midline. Although the flower is very small, it corresponds exactly to the flower found in may species of *Gladiolus*. This, together with a *Gladiolus*-like capsule and seeds typical of *Gladiolus* make it seem certain that *Geissorhiza bojeri* correctly belongs in *Gladiolus*. The finely fibrous corm tunics are also consistent with this placement, although such corm tunics are unusual in the genus. I have no hesitation in proposing the following combination:

Gladiolus bojeri (Baker) Goldbl. comb. nov. *Geissorhiza bojeri* Baker, J. Bot. new ser. 5:239. 1876: basionym. TYPES: Madagascar, Antoungoan Mts., Emirne, *Bojer s.n.* (K, lectotype, here designated); *Hilsenberg s.n.* (K, syntype, not seen).

2. *Geissorhiza ambongensis* Perrier. The second of the Madagascar Iridaceae assigned to *Geissorhiza* is *G. ambongensis* (Perrier, 1939). This species is quite different from *G. bojeri*. It is apparently rare and as far as I can tell is only known from two gatherings, both from low elevation along the central west coast. The plants are small, with stems up to 15 cm high, and have several, somewhat longer, broad, lanceolate, soft textured leaves. The spikes bear only one or two, long-tubed, orange flowers, which are well exerted from the herbaceous bracts. The description is not clear on this point, but the statement that the anthers are fixed dorsally suggests to me that the stamens may be unilateral and arched under the dorsal tepal, and hence the flowers are zygomorphic. The dried specimens support this interpretation. The capsules, not present on the specimens at my disposal, are described as spherical-trigonous, 8–10 mm in diameter, with 3–4 irregularly spherical seeds per loculus. The seeds are unequivocally stated to lack wings. The corm tunics are fibrous.

This species clearly does not belong in *Geissorhiza*. It is even less *Geissorhiza*-like than *G. bojeri*. However, its correct generic placement is uncertain. As the seeds are said to lack the wing, found in almost all species of *Gladiolus*, it does not seem well placed in this genus. The orange flower color, not found in *Geissorhiza* at all, and not common in *Gladiolus,* suggests *Tritonia* or *Crocosmia*, and other characters are consistent with these closely allied African genera, which incidentally are not recorded from Madagascar.

I would prefer not to assign *G. ambongensis* to either *Tritonia* or *Crocosmia* on the basis of present information, although it must be excluded from *Geissorhiza*. I hope that more material will become available to me in the future to assist with this problem. Live plants in particular are needed to determine chromosome

number, useful in the systematics of Iridaceae (Goldblatt, 1971), and to examine more details of the flower and fruit morphology.

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ILLINOIS SOLANACEAE IN THE MISSOURI BOTANICAL GARDEN HERBARIUM AND BIOGRAPHICAL SKETCHES OF SOME COLLECTORS

ROBERT H. MOHLENBROCK[1]

The herbarium of the Missouri Botanical Garden (MO), established in 1859 by Henry Shaw, when Shaw purchased the Bernhardi herbarium at Erfurth, Germany, on the recommendation of George Engelmann, ranks among the greatest herbaria in the world, not only in terms of numbers of specimens but also in historic importance.

Early collections in the Missouri Botanical Garden herbarium, many of them type specimens, were made by George Engelmann, Ferdinand Lindheimer, Nicholas Riehl, Charles A. Geyer, August Fendler, George Vasey, Elihu Hall, Samuel B. Mead, H. Eggert, A. W. Chapman, and others. Later, Robert Ridgway, Jesse M. Greenman, Ernest J. Palmer, Benjamin Franklin Bush, and Frank Seymour, among others, contributed some of their United States collections to the Missouri Botanical Garden. In more recent times, the vast Missouri collections of Julian A. Steyermark have been deposited at MO.

The purpose of this paper is to document every Illinois collection of the Solanaceae in MO. Critical notes on some specimens and on the taxonomy of certain taxa are included. Brief biographical sketches of the earlier collectors cited in this paper follow the taxonomic discussion. The research was conducted in conjunction with the author's overall treatment of the Solanaceae for The Illustrated Flora of Illinois project.

PHYSALIS L.

Nine species of *Physalis* from Illinois, including one previously unrecorded from Illinois, are in MO. The nomenclature for the Illinois *Physalis* used in this paper follows Mohlenbrock (1975). Most significant of the collections is a specimen of *P. texana* Rydb. The specimen, collected by George Engelmann from St. Clair County, represents the only known Illinois collection. This collection apparently has never been recorded in the literature, even though it bears an annotation label by P. A. Rydberg. Rydberg studied the United States species of *Physalia* during the last part of the nineteenth century. He published his findings in 1896 in the Memoirs of the Torrey Botanical Club. In that work, Rydberg described *P. texana* from Texas, citing a collection by Heller as the type. He also cited a Lindheimer collection from Texas, a duplicate of which is in MO, and annotated by Rydberg. It is interesting to note that although Rydberg had annotated the Illinois specimen "*P. texana* sp. nov. ?," he failed to cite the collection in his work. The Illinois specimen is extremely close in appearance to

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the Lindheimer collection from Texas. Waterfall (1958), in his treatment of the genus *Physalis* north of Mexico, considers *P. texana* to be a variety of *P. virginiana*.

Since a description of *P. texana* Rydb. does not appear in regional floras of the eastern and midwestern United States, it is described below. A photograph of the Illinois collection is found in Fig. 1.

Physalis texana Rydb. Mem. Torrey Bot. Club 4:339–340. 1896.

Physalis virginiana Mill. var. *texana* (Rydb.) Waterfall, Rhodora 60:153. 1958.

Perennial herb from an elongated root; stems low, more or less spreading to suberect, smooth or nearly so, angular, striate, to 30 cm long; leaves ovate, acute to obtuse at the tip, rounded at the asymmetrical base, usually entire, glabrous on both surfaces, to 4 cm long, on decurrent petioles; flowers solitary, axillary, borne on peduncles up to 1 cm long; calyx campanulate, 5-lobed, the lobes ovate, about as long as the tube; corolla up to 2 cm long, yellow with a dark center; anthers yellow; fruiting calyx up to 3 cm long, ovoid, more or less 10-angled, not sunken at the base; berries purple.

ST. CLAIR: Sandy banks along the Mississippi River, opposite St. Louis, August, 1841, *G. Engelmann s.n.*

In the Illinois flora, *Physalis texana* is most nearly related to *P. subglabrata* and *P. macrophysa*. All three species are glabrous perennials with ovate to ovate-oblong leaves and red or purple berries. *Physalis macrophysa* differs by its large fruiting calyx up to 6 cm long. *Physalis subglabrata,* which has smaller fruiting calyces, as does *P. texana,* has larger leaves, longer peduncles, and fruiting calyces sunken at the base.

Other Illinois collections of the genus *Physalis* in MO are:

Physalis heterophylla Nees var. **heterophylla**. COOK: *H. H. Babcock s.n.*; *J. M. Greenman 1973, 2044, 2802, 2821, 2880.* HENDERSON: *H. N. Patterson s.n.* KNOX: *J. Solomon 1122.* RICHLAND: *R. Ridgway 2185, 2187, 2451, 2465.* ST. CLAIR: *H. Eggert s.n.*; *G. Engelmann s.n.*; *A. S. Hitchcock s.n.*; *J. Norton s.n.* STARK: V. H. Chase 59-97. WABASH: *R. Ridgway 2585.*

Physalis heterophylla Nees var. **ambigua** (Gray) Rydb. COOK: *A. Chase 1482.* WABASH: *E. J. Palmer 15570.*

Physalis heterophylla Nees var. **nyctaginea** (Gray) Rydb. RICHLAND: *R. Ridgway 2581.*

Physalis ixocarpa Brotero. ST. CLAIR: *J. O Neill 5410.*

Physalis lanceolata Michx. COOK: *H. Babcock s.n.* MADISON: *Collector unknown #337.* PEORIA: *V. H. Chase 3570*; *J. R. Churchill s.n.* ST. CLAIR: *H. Eggert s.n.*

Physalis pendula Rydb. ALEXANDER: *E. J. Palmer 16489.* ST. CLAIR: *H. Eggert s.n.*; *F. Wislizenus 338.*

Physalis pruinosa L. ST. CLAIR: *H. Eggert s.n.*; *G. Engelmann s.n.*; *J. Neill 11402.*

Physalis pubescens L. HARDIN: *E. J. Palmer 19589.* ST. CLAIR: *H. Eggert s.n.*; *G. Engelmann s.n.*; *J. Neill 16099, 16791*; *R. J. Seibert 1142.*

Physalis subglabrata Mack. & Bush. CHAMPAIGN: *G. N. Jones 16594.* KANKAKEE: *E. E. Sherff 1636.* ST. CLAIR: *J. O. Neill 11175, 16258.* TAZEWELL: *V. H. Chase 3252, 17048.*

Physalis virginiana Mill. KANKAKEE: *O. E. Lansing & E. E. Sherff 3.* STARK: *V. H. Chase 595.*

FIGURE 1. (above) Herbarium specimen of *Physalis texana* Rydb., from St. Clair County, Illinois. (below) Label from specimen of *P. texana* from Illinois.

Nicotiana L.

Nicotiana in the midwestern states is usually represented by a few collections of *N. rustica* L., growing as an escape from cultivation. Rarely are any other species found as adventives. There is a specimen from Illinois, however, in MO of *N. longiflora,* a well defined species rarely found as an escape from cultivation in the eastern United States. The species was collected on July 9, 1858, by J. Norton in East St. Louis, where two plants were observed, according to the collection notes.

Because of the infrequency of this species in the eastern United States, and because descriptions of it are not found in regional floras, *Nicotiana longiflora* is characterized below. A photograph of the Illinois specimen is seen in Fig. 2.

Nicotiana longiflora Cav. Descr. Pl. 106. 1802.

Annual or perennial herb; stems erect, to 1 m tall, sparsely pubescent, rarely viscid; basal leaves in a rosette, oblanceolate to elliptic-ovate, pointed at the tip, tapering to the base into a winged petiole, slightly pubescent, up to 30(–50) cm long; cauline leaves lanceolate to lance-ovate, sessile, auriculate; inflorescence racemose, the flowers not overlapping; flowers mildly fragrant, borne on pedicels up to 20 mm long; calyx 5-lobed, the lobes subulate, about as long as the tube, the tube 10-nerved; corolla pale yellow, often tinged with purple, puberulent on the outside, 5-lobed, the lobes ovate, acute, the tube up to 12 cm long, up to 2.5 mm broad; capsule ovoid, 10–15 mm long, with ellipsoid seeds up to 0.5 mm long, light brown, reticulate.

ST. CLAIR: East St. Louis, July 9, 1858, *J. Norton s.n.*

Solanum L.

Solanum is represented by collections in MO of six of the eight species recorded from Illinois. The most significant collections of the genus are two made by Elihu Hall from Menard County, each representing the first collection of the species from Illinois. One is of *Solanum rostratum* Dunal, the other of *S. triflorum* Nutt. A collection by H. Eggert of *S. elaeagnifolium* from St. Clair County marks the southernmost record for this plant in Illinois.

The binomial *Solanum ptycanthum* Dun. is used below for plants usually referred to as *S. americanum* L. and *S. nigrum,* following Schilling (1981). *Solanum americanum* and *S. nigrum* are two distinct species, apparently not occurring in Illinois.

Solanum carolinense L. CLINTON: *W. D'Arcy 3424*. JACKSON: *J. McCree 1261*. KNOX: *J. Solomon 1145*. MADISON: *J. Solomon 3877*. MARION: *W. D'Arcy 3431*. RANDOLPH: *W. D'Arcy 3467*. RICHLAND: *R. Ridgway 2452*. ST. CLAIR: *H. Eggert s.n.*

Solanum dulcamara L. KNOX: *J. Solomon 1207*. PERRY: *H. Eggert s.n.*

Solanum elaeagnifolium Cav. ST. CLAIR: *H. Eggert s.n.*

Solanum ptycanthum Dun. ex DC. CHAMPAIGN: *G. N. Jones 17353*. COOK: *J. M. Greenman 2811*. JACKSON: *J. McCree 1265*. KNOX: *J. Solomon 1092*. ST. CLAIR: *J. O. Neill 16299*. WABASH: *R. Ridgway 2852*. WILLIAMSON: *J. McCree 798*.

FIGURE 2. (above) Herbarium specimen of *Nicotiana longiflora* L., collected in St. Clair County, Illinois. (below) Label from specimen of *N. longiflora* from Illinois.

Solanum rostratum Dunal. COOK: *J. R. Churchill s.n.*; *H. H. Smith 5755*. MENARD: *E. Hall 5879*. MONTGOMERY: *Hlaskan s.n.* RICHLAND: *R. Ridgway 2620*. ST. CLAIR: *H. Eggert s.n.*; *J. Norton s.n.* TAZEWELL: *V. H. Chase 3603*.

Solanum triflorum Nutt. MENARD: *E. Hall s.n.*

DATURA L.

Of the two species of *Datura* known from Illinois, only *D. stramonium* and its variety *tatula* are represented in MO.

Datura stramonium L. CHAMPAIGN: *G. N. Jones 17495*. KANKAKEE: *E. E. Sherff 1617, 1628*. MENARD: *O. E. Lansing & E. E. Sherff 67*. ST. CLAIR: *H. Eggert s.n.*; *J. H. Kellogg s.n.*; *J. O. Neill 15761*. TAZEWELL: *V. H. Chase 3605*.

Datura stramonium L. var. **tatula** (L.) Torr. KNOX: *J. Solomon 1135*. ST. CLAIR: *J. P. Bennett 41*.

HYOSCYAMUS L.

The escaped henbane, *Hyoscyamus niger* L., is the only member of the genus in Illinois, and it has not been collected during the twentieth century. The only Illinois specimen in MO has not been reported before in literature on the Illinois flora.

Hyoscyamus niger L. Northern Illinois: *G. Vasey 5924*.

LYCIUM L.

One of two species of matrimony vine known from Illinois is represented in MO.

Lycium halimifolium Mill. MADISON: *Minden s.n.* ST. CLAIR: *H. Eggert s.n.*; *L. H. Pammel s.n.* TAZEWELL: *V. H. Chase 3295*.

BRIEF BIOGRAPHICAL SKETCHES

HENRY HOMES BABCOCK (1832–1881) was born in Thetford, Vermont, and attended Dartmouth College from 1849–1851 before moving to Illinois. He collected about 10,000 specimens in Illinois. The bulk of his herbarium was given to Northwestern University in 1887, although a few specimens were given to the Missouri Botanical Garden.

MARY AGNES CHASE (1869–1963) was a native of Iroquois County, Illinois. After serving as a proofreader for the Chicago Inter Ocean, she was employed as an assistant botanist at the Field Museum of Natural History from 1901 to 1903. In 1903 she moved to Washington where she was employed by the United States Department of Agriculture, first as an agrostology artist until 1907, then as assistant systematic agrostologist from 1907 to 1918, and finally as agrostologist until her retirement. Some of her early collections are from Cook County, Illinois.

VIRGINIUS HEBER CHASE (1876–1966) was born in Wady Petra, Illinois, the great grandson of Philander Chase, an Episcopal bishop and founder of Kenyon College in Ohio and Jubilee College near Peoria, Illinois. At the age of 17, Virginius became interested in plants, and he and his aunt Agnes (see above) began

collecting and "keying out" plants on their own, a hobby he pursued for the remainder of his life. For a while, Chase served as telegraph operator in Wady Petra, and then built a grain elevator and conducted a successful business in lumber, drain tile, coal, and feed. For twenty-eight years he worked in the P. & P. U. railroad freight house at Peoria. In later years he also served as custodian of the Peoria Academy of Science. Chase made several thousand collections of plants, many of them from Peoria, Stark, Tazewell, and Woodford counties, Illinois. A part of his collection was sold to the Missouri Botanical Garden to help defray his collection expenses.

JOSEPH RICHMOND CHURCHILL (1845–1933) spent most of his life in Massachusetts but travelled and collected plants extensively in the United States as an avocation. After graduating from Harvard Law School in 1869, he practiced law in Boston with his father before being named judge of the Municipal Court, Dorchester District of Boston, a position he held for 60 years. During his life, he became a close friend of Jesse More Greenman of the Missouri Botanical Garden, a friendship that resulted in Churchill willing his herbarium to the Missouri Botanical Garden.

EARL DOUGLASS (1862–1931) was born in Medford, Minnesota. He received his B.S. from Iowa State College in 1893 and an M.S. from the University of Montana in 1900 in vertebrate paleontology before becoming a fellow at Princeton University from 1900 to 1902. In 1902, Douglass became a member of the Department of Vertebrate Paleontology at the Carnegie Museum, where he worked for the rest of his life. His most important contribution was the discovery of an important dinosaur fossil bed along the Green River in Utah, later to become known as Dinosaur National Monument. During 1890 and 1891, Douglass served as an assistant to Professor William Trelease at the Missouri Botanical Garden. It was during this brief period that he made a few plant collections in Illinois.

HEINRICH KARL DANIEL EGGERT (1841–1904) was born in Osterwieck, Germany, and he served as a public teacher in Magdeburg for a few years before coming to the United States in 1873 to seek his fortune. He worked on a farm in southern New York for a few months prior to coming to the St. Louis area. Unable to find suitable employment, he became a newspaper deliveryman, a profession he followed for twenty years. During this time, he became a close friend of Dr. George Engelmann, who encouraged Eggert's interest in plant collecting. Eggert collected hundreds of plants from St. Clair County, Illinois, during his life. He also collected large quantities of seeds of native grapevines, which he sent to Europe to stock European vineyards that had been depleted by the fungus *Phylloxera*. His herbarium of 60,000 specimens is in MO.

GEORGE ENGELMANN (1809–1884), the oldest of thirteen children, was born in Frankfurt-am-Main, Germany. He obtained an M.D. degree from Wuerzburg in 1831, his doctoral dissertation being on the abnormalities in plants and their relationships to morphology. For a few months, he studied botany in Paris with the German botanist Alexander Braun. In 1832, Engelmann sailed for the United States where his family owned land in the Mississippi Valley. Engelmann moved in with his cousin in Belleville, Illinois, in February 1833. After two-and-one-half

years, he moved to St. Louis, where he began practicing medicine and pursuing his hobbies of botany and meteorology. He was a highly successful and respected physician from 1835 to 1884. Engelmann chose to work on plant groups considered to be difficult—Cactaceae, *Cuscuta, Juncus, Vitis, Yucca, Agave, Quercus, Pinus, Abies,* and *Juniperus*. In the early 1840s, Engelmann instructed August Fendler in botanical matters so that Fendler could become curator of Henry Shaw's botanical garden herbarium. After Engelmann's death, his son presented Dr. Engelmann's herbarium of 40,000 specimens to the Missouri Botanical Garden. Several of Engelmann's collections were from St. Clair County, Illinois.

KARL ANDREAS GEYER was born in Dresden, Germany, on November 30, 1809. At the age of 21, Geyer began working at the Dresden Botanic Garden where he was employed until he left for America in 1834. He was with the Nicollet expedition surveying the country between the Missouri and Mississippi rivers in 1836. It was during 1840 and part of 1841 that he collected in the St. Louis area on both sides of the Mississippi and along the Illinois River as far northeast as Cass County. During this time he became a good friend of Dr. George Engelmann. From 1841 to 1844, he explored from Missouri to the Pacific Coast, leaving for Europe by boat on November 13, 1844. He returned to work at the Dresden Botanic Garden where he remained until his death on November 21, 1853.

NOAH MILLER GLATFELTER (1837–1911) was another prominent plant collector in the St. Louis area. Born in York County, Pennsylvania, Glatfelter received his medical degree from the University of Pennsylvania in 1864, and shortly thereafter became the Assistant Surgeon of United States Volunteers. After the Civil War, Glatfelter settled in the St. Louis area and began his private medical practice. It was not until 1889 that he became engrossed in the study of plants, collecting vascular plants and fungi extensively in the St. Louis area. He became known as an authority on the genus *Salix*.

JESSE MORE GREENMAN (1867–1951), born in North East, Pennsylvania, received degrees from the University of Pennsylvania and Harvard before obtaining his Ph.D. in Berlin in 1901. After serving as Assistant Curator in the Department of Botany at the Chicago Natural History Museum and Assistant Professor of Botany at the University of Chicago, he became Curator of the Herbarium at the Missouri Botanical Garden and Professor of Botany at Washington University, positions he held from 1913 to 1948. Some Greenman collections are from northern Illinois.

ELIHU HALL (1822–1882), a native of Patrick County, Virginia, was trained as a surveyor. For much of his life, he served as surveyor of Menard County, Illinois, as well as being a farmer. As an amateur botanist, Hall collected many plants that were new for Illinois, including a few species new to science. In 1858, he helped organize the Illinois Natural History Society in Bloomington. In addition to collecting plants, Hall painted both plants and animals. In the later years of his life, Hall made an extensive collection of fresh water and land snails of Illinois.

ALBERT SPEAR HITCHCOCK (1865–1935), born in Owasso, Michigan, received three degrees from Iowa State College. For a decade, he was Professor of Botany

at Kansas State College before becoming agrostologist at the United States National Herbarium, a position he held from 1901 to 1935. After studying at various European herbaria in 1935, Hitchcock died at sea en route home on "The City of Norfolk." A few Hitchcock collections are from Illinois.

HENRI THEODORE ANTOINE DELENG HUS (1876–?) was born in Leyden, Holland, on May 14, 1876. While still a youth, Hus came to America where he obtained bachelor's and master's degrees at the University of California and a doctorate in 1908 at Washington University in St. Louis. He was employed as an experimenter at the Missouri Botanical Garden from 1905 to 1908. It was during this time he made a few collections of plants from Illinois. In 1908 he became an employee of the New York Botanical Garden.

JOHN HENRY KELLOGG (1862–1939), a St. Louisan all his life, was a gardener at the Missouri Botanical Garden from 1900 to 1931. He learned about native plants from Geoge Letterman, and both he and Letterman collected extensively in the Allenton, Missouri, area. Kellogg was an active member of the St. Louis Wild Flower Club. Only a few of his collections are from Illinois.

ODELLE EDWARD LANSING (1867–1918) collected in northern Illinois while employed as assistant botanist at the Field Museum.

GEORGE WASHINGTON LETTERMAN (1841–1913), born in Bellefonte, Pennsylvania, interrupted his schooling at State College in Center County, Pennsylvania, to enlist in the Union Army during the Civil War. After the war, Letterman settled in Allenton, Missouri, a few miles west of St. Louis. He taught in the public school system for twenty years and then served two years as superintendent of schools of St. Louis County. He became interested in woody plants through his friendship with August Fendler and Dr. George Engelmann. In 1880 he was appointed by the United States government to collect data on trees and forests in Missouri, Arkansas, and parts of Louisiana and Texas. Later he collected tree specimens for the American Museum of Natural History's Jesup Collection of North American Woods. He collected frequently in the Allenton, Missouri, area with John Henry Kellogg. Only a few of Letterman's collections are from Illinois.

FRANCIS EUGENE MCDONALD (1860–1920), born in Wyanet, Illinois, moved at an early age to Peoria where he resided for the remainder of his life. Although he studied law and was admitted to the bar on January 8, 1883, he was not excited about the legal profession. When his father became ill, McDonald took his place as a railway mail clerk, a position which became permanent in 1884 and which he held until his death. McDonald collected plants as a hobby, mostly in the Peoria area.

WILL SAYER MOFFATT (1847–1941) obtained a medical degree from Hahnemain Medical College in 1868 and practiced medicine in Chicago while living in Wheaton. He was a frequent collector of flowering plants and fungi in the Chicago area, often in the company of H. S. Pepoon. Moffatt published works on the higher fungi of the Chicago region. On his retirement from the medical profession in 1927, he moved to Los Angeles where he resided until his death.

ERNEST JESSE PALMER (1875–1962) was born in Leicester, England. As a railroad worker in Webb City, Missouri, Palmer had an early interest in geology and botany. From 1913 to 1948, he was a field collector for the Missouri Botanical Garden and the Arnold Arboretum. Palmer made one extensive trip across southern Illinois in 1919.

LOUIS HERMAN PAMMEL (1862–1931) was born in LaCrosse, Wisconsin. After receiving a bachelor's degree from the University of Wisconsin in 1885, Pammel studied in the Farlow Laboratory of Harvard University before enrolling in the Henry Shaw School of Botany at Washington University. He completed his doctorate under the direction of William Trelease. For forty years, Pammel was head of the Department of Botany at Iowa State College. He wrote the Iowa conservation bill and served as the first chairman of the Iowa Conservation Board. Although Pammel collected primarily in the Rocky Mountains, he did make a few excursions into Illinois.

HENRY NORTON PATTERSON (1853–1919) lived most of his life in Oquawka, Illinois, the place of his birth. He was a printer by trade, specializing in printing botanical lists and labels. Patterson collected extensively in the Oquawka area, as well as in Colorado.

ROBERT RIDGWAY (1850–1929) was born in Mt. Carmel, Illinois, and died in Olney, Illinois. In between, he carved out an illustrious career as an ornithologist and botanist. He also developed a standard color chart that is still in use today. Most of his Illinois plant collections are from Wabash County, Illinois.

JACOB SCHNECK (1843–1906) was a native of New Harmony, Indiana. Schneck taught school for a short time in Olney, Illinois, until he enrolled in the Chicago Medical College where he received his M.D. in 1871. Until his death in 1906, he practiced medicine in Mt. Carmel, Illinois. He spent much of his free time collecting plants in the Wabash Valley of Illinois, near his home.

EARL EDWARD SHERFF (1886–1966) was a professionally trained botanist, receiving a bachelor's degree from Albion College and the masters and doctorate from the University of Chicago. After teaching in high schools at Elgin, Deerfield (Highland Park), Christian Fenger (Chicago), and Lindblom Technical High (Chicago), he taught at Chicago Teachers College and was a Research Associate at the Chicago Natural History Museum. He collected extensively in the Chicago area, often in the company of O. E. Lansing.

HURON HERBERT SMITH (1883–1933), a native of Danville, Indiana, obtained a bachelor's degree from DePauw University and a master's degree from Cornell University. From 1917 to 1933, Smith was Curator of Botany at the Milwaukee Public Museum until he was tragically killed when his car was hit by a train in Glenview, Illinois. In addition to collecting plants in the Chicago area, he was an authority on Indian life and was made a member of the Menominee tribe.

LEVI MENGER UMBACH (1853–1918) was born on July 15, 1853, in Ontario. After receiving his college degree from Northwestern College of Naperville, Illinois, in 1877, he returned to the college where he was professor of physical and

biological sciences from 1884 to 1918. He collected many specimens of vascular plants from the Chicago region and from JoDaviess County, Illinois.

GEORGE VASEY (1822–1893) was born in Scarborough, Yorkshire, England. In 1848, he obtained his medical degree from the Berkshire Medical Institute in Pittsfield, Massachusetts. He practiced medicine in Elgin (Kane County) and Ringwood (McHenry County), Illinois, from 1848 to 1866. In 1868, he went on the Powell expedition to Colorado as a botanist. From 1869 to 1872, he was Curator of the Natural History Museum at Normal, Illinois, until he was appointed Botanist at the United States Department of Agriculture in Washington, D.C. Among his vast collections are many specimens from northeastern Illinois.

FRIEDRICH ADOLPH WISLIZENUS (1810–1889) was born in Königsee, Schwarzburg Rudolstadt, Germany. After receiving his medical degree from Zurich in 1834, he sailed for New York in 1835 to practice medicine. After two years, he moved to Mascoutah, Illinois, where he also collected plants. In 1839 he moved to St. Louis and became a close friend of Dr. George Engelmann. Engelmann left his medical profession in Wislizenus' hands when he went on botanical excursions. Wislizenus, himself, collected extensively in the southwestern United States and was a member of several expeditions.

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ILLINOIS CONVOLVULACEAE IN THE MISSOURI BOTANICAL GARDEN HERBARIUM

ROBERT H. MOHLENBROCK[1]

In an earlier paper on the Illinois Solanaceae in the herbarium of the Missouri Botanical Garden, Mohlenbrock (1982) showed that the collections were not only important historically but they included some previously unreported records. Similar results have been obtained when Illinois collections of the Convolvulaceae have been examined in conjunction with the author's study for *The Illustrated Flora of Illinois*. The collections of Convolvulaceae are particularly enhanced by the George Engelmann specimens of *Cuscuta*, made in conjunction with Engelmann's monographic treatment of that genus in 1842 and 1859.

In this paper, all specimens of Convolvulaceae from Illinois in the herbarium of the Missouri Botanical Garden are cited, along with critical notes on some of the specimens. Nomenclature for the taxa essentially follows Mohlenbrock (1975). Brief biographical sketches of some of the early collectors are given in Mohlenbrock, 1982.

CALYSTEGIA R. Br.

Although the taxa of *Calystegia* listed below are sometimes included in the genus *Convolvulus*, I am recognizing them in the segregate genus *Calystegia*, following the evidence presented by Brummitt (1965) and Lewis & Oliver (1965). *Calystegia* differs from *Convolvulus* by the surface configurations of the pollen grains, by the unilocular ovary, and by a pair of broad bracteoles immediately below the sepals.

In my *Guide to the Vascular Flora of Illinois* (1975), I recognized *Calystegia pubescens*, *C. spithamaea*, and three varieties of *C. sepium*. Among the latter is var. *fraterniflora*. After studying the material in the Missouri Botanical Garden herbarium, I have been convinced to follow Brummitt (1980), who has described two additional subspecies of *C. sepium* and who has transferred var. *fraterniflora* to a subspecies of *C. silvatica*. The holotype of Brummitt's *C. sepium* ssp. *erratica* is a Robert Ridgway collection from Richland County, Illinois, deposited in MO.

Calystegia sepium (L.) R. Br., the common bindweed in Illinois, is comprised of four subspecies, two of which have been recently described by Brummitt (1980). Since Brummitt's two new North American subspecies have not been "keyed out" or described in floristic literature of this continent, a key to the four subspecies in Illinois and a description of the two most recently described subspecies are given below.

KEY TO THE SUBSPECIES OF *CALYSTEGIA SEPIUM* IN ILLINOIS

1a. Bracteoles not clearly distinct from the sepals, forming a continuous spiral with the sepals and gradually merging with them; sinus of leaves strongly occluded. ---- *C. sepium* ssp. *erratica*

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1b. Bracteoles clearly differentiated from the sepals, never merging with them; sinus of leaves open or rarely only slightly occluded.
  2a. Plants glabrous or sparsely pubescent; leaves mostly hastate.
    3a. Leaves with V-shaped sinus; corolla pink. ---------- *C. sepium* ssp. *americana*
    3b. Leaves with U-shaped sinus; corolla white (rarely suffused with pale rose). ---------- *C. sepium* ssp. *angulata*
  2b. Plants densely soft-pubescent; leaves sagittate. ---------- *C. sepium* ssp. *repens*

Calystegia sepium (L.) R. Br. ssp. **erratica** Brummitt, Kew Bull. 35(2):330. 1980.

Plants glabrous or often pubescent; lobes of leaves truncate, scarcely spreading; sinus of leaves strongly occluded; bracteoles not clearly distinct from the sepals but forming a continuous spiral with the sepals and gradually merging with them; bracteoles green, acute to subobtuse, carinate, 1.6–2.6 cm long, 1.0–2.4 cm broad; corolla rose, 4.3–6.0 cm long; stamens 2.5–3.0 cm long.

The holotype designated by Brummitt (1980) for ssp. *erratica* is *R. Ridgway 2397* from Richland County, Illinois, and deposited in the herbarium of the Missouri Botanical Garden. The type was collected about ten miles northeast of Olney on May 25, 1925 (Fig. 1).

Other states and provinces cited by Brummitt for ssp. *erratica* are Indiana, Michigan, Pennsylvania, New Jersey, New York, and Ontario. An adventive specimen from Oregon is also cited. Two other specimens of ssp. *erratica* are in MO, one being from Michigan and one from Pennsylvania.

Subspecies *erratica* differs from all other subspecies of *C. sepium* by its bracteoles, which form a continuous spiral and merge imperceptibly into the sepals so that each flower appears to be subtended by 3–4 bracteoles, rather than two.

Calystegia sepium (L.) R. Br. ssp. **americana** (Sims) Brummitt, Ann. Missouri Bot. Gard. 52:216. 1965.

Convolvulus sepium L. var. *americanus* Sims, Bot. Mag. 19:pl. 732. 1804.
Convolvulus americanus (Sims) Greene, Pittonia 3:328. 1898.
Calystegia sepium (L.) R. Br. var. *americana* (Sims) Kitagawa, Rep. Inst. Sci. Res. Manchoukuo 3 App. 1:365. 1939.
Convolvulus sepium L. var. *communis* Tryon, Rhodora 41:419. 1939.

Subspecies *americana* is distinguished from ssp. *angulata* by the V-shaped sinus between the basal lobes of the leaf and by its usually pink flowers. The two subspecies show some intergradation, although most specimens can be assigned readily to one subspecies or the other.

The following Illinois collections of *C. sepium* ssp. *americana* are in MO:

ALEXANDER: *J. S. Huston 392*. COOK: *J. M. Greenman 1874, 1920*; *Jensen s.n.*; *H. H. Smith 5972*; *B. Venrick 3*.

Calystegia sepium (L.) R. Br. ssp. **angulata** Brummitt, Kew Bull. 35(2):328. 1980.

Plants glabrous; lobes of leaves triangular, spreading; sinus of the leaves U-shaped; bracteoles green, conspicuously carinate, acute, 1.2–3.2 cm long, 0.6–1.8 cm broad; corolla white or rarely tinged with pale rose, 2.8–6.4 cm long; stamens 1.9–3.1 cm long.

Until Brummitt described this subspecies, it was hidden within ssp. *americana*. It is more of a western subspecies, with Brummitt (1980) giving its range

FIG. 1. (above). Holotype of *Calystegia sepium* (L.) R. Br. ssp. *erratica* Brummitt, from Richland County, Illinois. (below) Label from holotype of *C. sepium* ssp. *erratica*.

to include the northern Pacific states and British Columbia through the Rocky Mountains to the Great Plains and Prairies, then sparingly eastward to New England and eastern Canada. The type is from Idaho.

Two collections of ssp. *angulata* from Illinois are in MO:

COOK: *J. M. Greenman 1961* (Fig. 2). WOODFORD: *G. N. Jones 14316*. The corolla of the Woodford County specimen is pink-tinged.

In addition to the two Illinois specimens of ssp. *angulata* in Illinois, there are specimens in MO from Colorado, Iowa, Kansas, Missouri, Nebraska, New Mexico, New York, Ohio, Pennsylvania, South Dakota, Washington, Wisconsin, Wyoming, the District of Columbia, British Columbia, and Saskatchewan.

Calystegia silvatica (Kit.) Griseb. ssp. **fraterniflorus** (Mack. & Bush) Brummitt, Kew Bull. 35(2):332. 1980.

Convolvulus sepium L. var. *fraterniflorus* Mack. & Bush, Man. Fl. Jackson Co., Mo. 153. 1902.
Convolvulus fraterniflorus (Mack. & Bush) Mack. & Bush, Annual Rep. Missouri Bot. Gard. 16:104. 1905.
Calystegia fraterniflora (Mack. & Bush) Brummitt, Ann. Missouri Bot. Gard. 52:216. 1965.
Calystegia sepium (L.) R. Br. var. *fraterniflora* (Mack. & Bush) Shinners, Sida 3:282. 1968.

This taxon usually has been considered either a distinct species or a variety of *Calystegia sepium*, differing primarily by its peduncles, or most of them, shorter than its petioles. Brummitt (1980) now indicates that because of its saccate, overlapping, obtuse bracteoles, it is more nearly related to *Calystegia silvatica*, rather than *C. sepium*, calling it *C. silvatica* ssp. *fraterniflora*.

The following specimens are in MO:

JACKSON: *J. McCree 819*. HANCOCK: *S. B. Mead s.n.*, in 1842. ST. CLAIR: *J. O. Neill 15273*. WABASH: *R. Ridgway 2234, 2432*.

Calystegia spithamaea (L.) Pursh. JO DAVIESS: *G. N. Jones 15803*. PEORIA: *V. H. Chase 3909*; *J. R. Churchill s.n.*

CONVOLVULUS L.

As a result of this study, a second species of *Convolvulus* has been found from Illinois that apparently has been undetected for nearly a century. *Convolvulus incanus* can now be added to the common and widespread *C. arvensis* in the Illinois flora. Since *C. incanus* occurs primarily in the southwestern United States and is not described in midwestern floras, a description of this species is presented below.

Convolvulus incanus Vahl, Sym. Bot. 3:23. 1794.

Trailing perennial; stems cinereous-pubescent, branched from the base; leaves oblong to elliptic, more or less rounded at the tip, tapering to a short petiole, cinereous-pubescent, up to 2.5 cm long; flowers 1–several from the axils of the leaves; sepals 5, more or less free, green, up to 8 mm long; corolla white, up to 1.2 cm across, with 5 acute lobes; capsule ovoid, up to 5 mm long, splitting at maturity into several valves.

ST. CLAIR: Along railroad north of East St. Louis, *N. M. Glatfelter* (?) *s.n.*—Fig. 3.

CALYSTEGIA Sepium (L.) R. Br.
subsp. angulata Brummitt
Ind
R. K. Brummitt R. 1973

PLANTS OF ILLINOIS.
HERBARIUM OF J. M. GREENMAN.
No. 1961
Convolvulus Sepium, L.
Along the Rock Island R. R.
via: 91st Street, Chicago
Collected by JMG 28 July 1907

PLANTS OF ILLINOIS.
HERBARIUM OF J. M. GREENMAN.
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Convolvulus Sepium, L.
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via: 91st Street, Chicago
Collected by JMG 28 July 1907

FIG. 2. (above) Herbarium specimen of *Calystegia sepium* (L.) R. Br. ssp. *angulata* Brummitt, from Cook County, Illinois. (below) Label from specimen of *C. sepium* ssp. *angulata* from Illinois.

Although no collector's name appears on the label of this specimen, the printed label indicates the specimen was in the herbarium of N. M. Glatfelter (and presumably the plant was collected by him). *Convolvulus incanus* is a species of the western United States that rarely becomes adventive east of the Mississippi River. Dr. Hans Hallier annotated the specimen in 1906 as *C. incanus*.

Convolvulus arvensis L. COOK: *H. H. Smith 5713*; *B. Venrick 28*. KNOX: *J. Solomon 974*. MADISON: *J. Solomon 3881*. PEORIA: *V. H. Chase 3130*. RICHLAND: *R. Ridgway 2621*. ST. CLAIR: *H. Eggert s.n.*

CUSCUTA L.

Dr. George Engelmann's first major contribution to North American botany was his work with the genus *Cuscuta*, which resulted in a preliminary treatise in 1842 and a comprehensive monograph in 1859. Engelmann made several collections of *Cuscuta*, beginning in 1835, shortly after his arrival in St. Louis. These provided an important basis for his study, and are critical material for the genus *Cuscuta*. Several of these are from Illinois.

Cuscuta cephalanthi Engelm.

This is one of Engelmann's new species, based on a specimen from St. Louis. The earliest Illinois collection apparently is that of Karl A. Geyer from Cass County, made in September, 1842. Engelmann's first collection of this species from Illinois was made in St. Clair County, in September, 1845. Collections of this species from Illinois are:

CASS: *K. A. Geyer s.n.*, in 1842. COOK: *E. E. Sherff 1896*. HENDERSON: *H. H. Patterson s.n.* MCHENRY: *G. Vasey 1*. MENARD: *E. Hall s.n.* ST. CLAIR: *G. Engelmann s.n.*, in 1845.

Cuscuta compacta Juss. ST. CLAIR: *H. Eggert s.n.*; *G. Engelmann s.n.*, in August, 1845.

Cuscuta coryli Engelm.

Engelmann named *C. coryli* and its var. *stylosa* in 1842 and, a few years later, he named *C. inflexa*. All three of these taxa appear to represent morphological variations within the same species, *C. coryli*. The types for *C. coryli* and *C. inflexa* are from St. Louis, while the type for var. *stylosa* is from St. Clair County, Illinois, based on an 1838 collection made by Dr. Engelmann. Specimens of *C. coryli* from Illinois in MO are:

CASS: *K. A. Geyer s.n.*, in August, 1842. COOK: *J. M. Greenman 2782*; *E. E. Sherff s.n.* MENARD: *E. Hall 4*. ST. CLAIR: *G. Engelmann s.n.*, in August, 1838, as *C. coryli* var. *stylosa*; *G. Engelmann s.n.*, as *C. inflexa*; *H. Hus s.n.*; *T. Meyer s.n.*

Cuscuta cuspidata Engelm. PEORIA: *N. M. Glatfelter s.n.* ST. CLAIR: *H. Eggert s.n.* UNION: *S. Poellot 3076a*.

Cuscuta glomerata Choisy. COOK: *J. R. Churchill 673*; *J. M. Greenman 2881*; *E. E. Sherff 1755*. DU PAGE: *L. M. Umbach s.n.* IROQUOIS: *W. S. Moffatt 526*. MADISON: *E. Douglass s.n.* PEORIA: *V. H. Chase 3625*. ST. CLAIR: *H. Eggert s.n.* TAZEWELL: *V. H. Chase 3255*.

Cuscuta gronovii Willd.

Two rather distinct varieties of *C. gronovii* occur in the northeastern United States. Typical var. *gronovii* has calyx lobes shorter than the cylindrical corolla.

FIG. 3. (above) Herbarium specimen of *Convolvulus incanus* Vahl, from St. Clair County, Illinois. (below) Label from specimen of *C. incanus* from Illinois.

Apparently unaware of the existence of Willdenow's *C. gronovii,* Engelmann (1842) described *C. vulvivaga* for material identical with *C. gronovii* var. *gronovii*. Apparently the earliest collection of *C. gronovii* var. *gronovii* from Illinois is by Karl A. Geyer from Cass County, collected in September, 1842, and determined by Engelmann as *C. vulvivaga*.

Variety *latiflora* Engelm. differs from var. *gronovii* by the calyx lobes about as long as the campanulate corolla. Engelmann (1842) originally described this taxon as a species, calling it *C. saururi,* designating the type from St. Clair County, Illinois (margins of lakes, American Bottoms, opposite St. Louis, Karl A. Geyer, in September, 1841). In 1859, Engelmann changed the status of this taxon to a variety, calling it *C. gronovii* var. *latiflora*. Both var. *gronovii* and var. *latiflora* are recognized in today's Illinois flora. Specimens in MO of these two taxa are:

var. **gronovii**. ALEXANDER: *J. S. Huston 191*. CASS: *K. A. Geyer s.n.* KANE: *E. E. Sherff 1813, 1979*. MACON: *R. G. Mills 28*. MADISON: *R. H. Larner s.n.* MENARD: *E. Hall 1*. PEORIA: *V. H. Chase 3621*. RICHLAND: *R. Ridgway 2021, 2199*. ST. CLAIR: *M. Craig s.n.*; *H. Eggert s.n.*; *G. Engelmann s.n.*, in September, 1833, in August, 1845; *N. M. Glatfelter s.n.*; *A. S. Hitchcock s.n.*; *J. H. Kellogg s.n.*; *L. H. Pammel s.n.* STARK: *V. H. Chase 169*. WABASH: *J. Schneck s.n.* WASHINGTON: *F. Beckwith 46*. WAYNE: *R. Ridgway 1570*.

var. **latiflora** Engelm. ST. CLAIR: *H. Eggert s.n.*; *G. Engelmann s.n.* in August, 1845, and September, 1845; *K. A. Geyer s.n.* (the type of *C. saururi*).

Cuscuta indecora Choisy. ST. CLAIR: *H. Eggert s.n.*; *J. O. Neill 16522*.

Cuscuta pentagona Engelm.

Engelmann described *C. pentagona* in 1842, choosing a specimen from Virginia as the type. Three years later he named var. *microcalyx* from Illinois material which had smaller calyces. The two taxa are considered today to be equivalent.

CASS: *K. A. Geyer s.n.*, in July, 1842. HANCOCK: *F. Beckwith 45*. ST. CLAIR: *J. M. Greenman 4595*.

Cuscuta polygonorum Engelm.

The type for Engelmann's *C. polygonorum,* named in 1842, is a Lindheimer collection made in August, 1839, in St. Louis and deposited in MO. In 1845, Engelmann described green-fruited specimens otherwise referable to *C. polygonorum* as *C. chlorocarpa*. *Cuscuta polygonorum* and *C. chlorocarpa* have proven to be applicable to the same species.

PEORIA: *V. H. Chase 3322*. ST. CLAIR: *E. Douglass s.n.*; *H. Eggert s.n.*; *G. Engelmann s.n.*, in August, 1845. All three St. Clair County specimens were called *C. chlorocarpa* by Engelmann. TAZEWELL: *V. H. Chase 3313*.

IPOMOEA L.

All five species of Illinois ipomoeas are represented in MO. Although each species is distinct and requires no taxonomic discussion here, a few older specimens are exceptional. Geyer's collection of *I. lacunosa* from St. Clair County in September, 1841, is noteworthy because of its very early collection date, as are specimens by Wislizenus of *I. lacunosa* and *I. purpurea*.

Ipomoea coccinea L. RICHLAND: *R. Ridgway 1429.*

Ipomoea hederacea Jacq. CHAMPAIGN: *G. N. Jones 16264.* ST. CLAIR: *J. P. Bennett 38, 45*; *H. Eggert s.n.*; *J. M. Greenman 4206*; *J. O. Neill 11152.*

Ipomoea lacunosa L. ALEXANDER: *J. S. Huston 316.* HENDERSON: *H. N. Patterson s.n.* JACKSON: *J. McCree 1136, 1264.* MADISON: *F. W. Wislizenus 328.* PEORIA: *F. E. McDonald s.n.* RICHLAND: *R. Ridgway 2279.* ST. CLAIR: *H. Eggert s.n.*; *K. A. Geyer s.n.*, in September, *1841*; *N. M. Glatfelter 369*; *J. M. Greenman 4036, 4207*; *J. H. Kellog s.n.*; *G. W. Letterman s.n.*; *J. O. Neill 11025*; *L. H. Pammel s.n.*

Ipomoea pandurata (L.) Meyer. CHAMPAIGN: *G. N. Jones 16439.* COOK: *A. Chase 1390.* FRANKLIN: *T. S. Elias 1476.* KANKAKEE: *J. M. Greenman s.n.* ST. CLAIR: *H. Eggert s.n.*; *A. S. Hitchcock s.n.*; *J. O. Neill 10953.* STARK: *V. H. Chase 711.*

Ipomoea purpurea (L.) Lam. CHAMPAIGN: *G. N. Jones 14423.* JACKSON: *J. McCree 1289.* MCLEAN: *J. S. Solomon 144.* PIATT: *G. N. Jones 40918.* ST. CLAIR: *H. Eggert s.n.*; *F. Wislizenus 326.* VERMILION: *G. N. Jones 15489.*

STYLISMA Raf.

Stylisma is a genus of six species in temperate North America. The one taxon in Illinois has sometimes been placed in *Breweria,* but Myint, who revised the genus in 1966, has given reasons for recognizing *Stylisma.*

Stylisma pickeringii (Torr.) Gray var. **pattersonii** (Fern. & Schub.) Myint.

This variety was discovered in the sand prairies of Henderson County, Illinois, by H. N. Patterson on August 11, 1873. An isotype is in MO.

HENDERSON: Prairies near Oquawka, *H. N. Patterson s.n.*

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THREE NEW SPECIES OF *APHELANDRA* (ACANTHACEAE) FROM CENTRAL AMERICA[1]

LUCINDA A. MCDADE[2]

ABSTRACT

The newly described species are Central American members of the *Aphelandra pulcherrima* complex (Acanthaceae). *Aphelandra panamensis* McDade occurs in cloud forests at middle elevations in central and eastern Panamá. *Aphelandra golfodulcensis* McDade is found in southwestern Costa Rica and adjacent Panamá at low to middle elevations. *Aphelandra leonardii* McDade is known from the lowlands of eastern Panamá and from middle elevations in central Costa Rica.

The *Aphelandra pulcherrima* complex is a morphologically well-defined group of about 35 species found in South and Central America. Features distinguishing these species from other *Aphelandra* include extrafloral nectaries on the floral bracts and a distinctive corolla morphology (Leonard, 1953; McDade, 1980). In the course of revisionary work on the Central American species of this complex (McDade, 1980), three new species belonging to the group were discovered.

Aphelandra panamensis McDade, sp. nov. TYPE: Panama, Panamá, Slopes of Cerro Jefe, past Goofy Lake and large coffee finca, 800 m elev., *McDade 411* (DUKE, holotype; F, MO, isotypes).—FIG. 1.

Frutex 1–6 m altus; foliis ellipticis, 15–18 (22) cm longis, 3–6.5 cm latis. Inflorescentiae spicatae, terminales, sessiles, 1–5, 4–12 cm longae, 0.8–1.2 cm latae; rachis dense pubescens; bracteae imbricatae, rhombeo-ovatae, dentatae, 11–15 mm longae, 6–8 mm latae, virides vel sordide aurantiacae, nectaria 5–10 glandibus, glandes singulae 0.5 mm longae, 0.3 mm latae; bracteolae lanceolatae, 6–10 mm longae, 1.5–2.5 mm latae. Calycis lobi lanceolati vel anguste-ovati, 8–12 mm longi, 1.5–5 mm lati; corolla rubra, 5.5–7.0 cm longa, tubo 5 cm longo, labium superum 14–20 mm longum, 6–8 mm latum, lobus medius labi inferiores 18–23 mm longu, 4–7 mm latu; antherae 4–5 mm longae; stigma obliquum et cavum. Fructus immaturi sordide aurantiaci, 16–19 mm longi, 4.5–6.5 mm lati, 5.5–7 mm crassi; seminae atrobrunneae, orbiculares, 4–6 mm in diam., 2–3 mm crassae. Germinatio semihypogaea.

Shrubs or small trees 1–6 m high, sparsely branched; stems terete, younger stems densely pubescent, the trichomes upwardly appressed, white, 0.5–0.75 mm long, older surfaces glabrate. Leaves opposite, narrowly elliptic, 15–18(–22) cm long, 3–6.5 cm wide, apically acuminate to acute, basally attenuate and decurrent on the petiole, marginally entire or undulate, the upper surface of youngest leaves sparsely pubescent, glabrate with age, lower surface moderately pubescent, the trichomes appressed, white, about 0.5 mm long; petioles lacking or to 5 mm long, densely pubescent, the trichomes erect, white, about 0.5 mm long; uppermost leaves subtending inflorescences frequently reduced. Inflorescences terminal,

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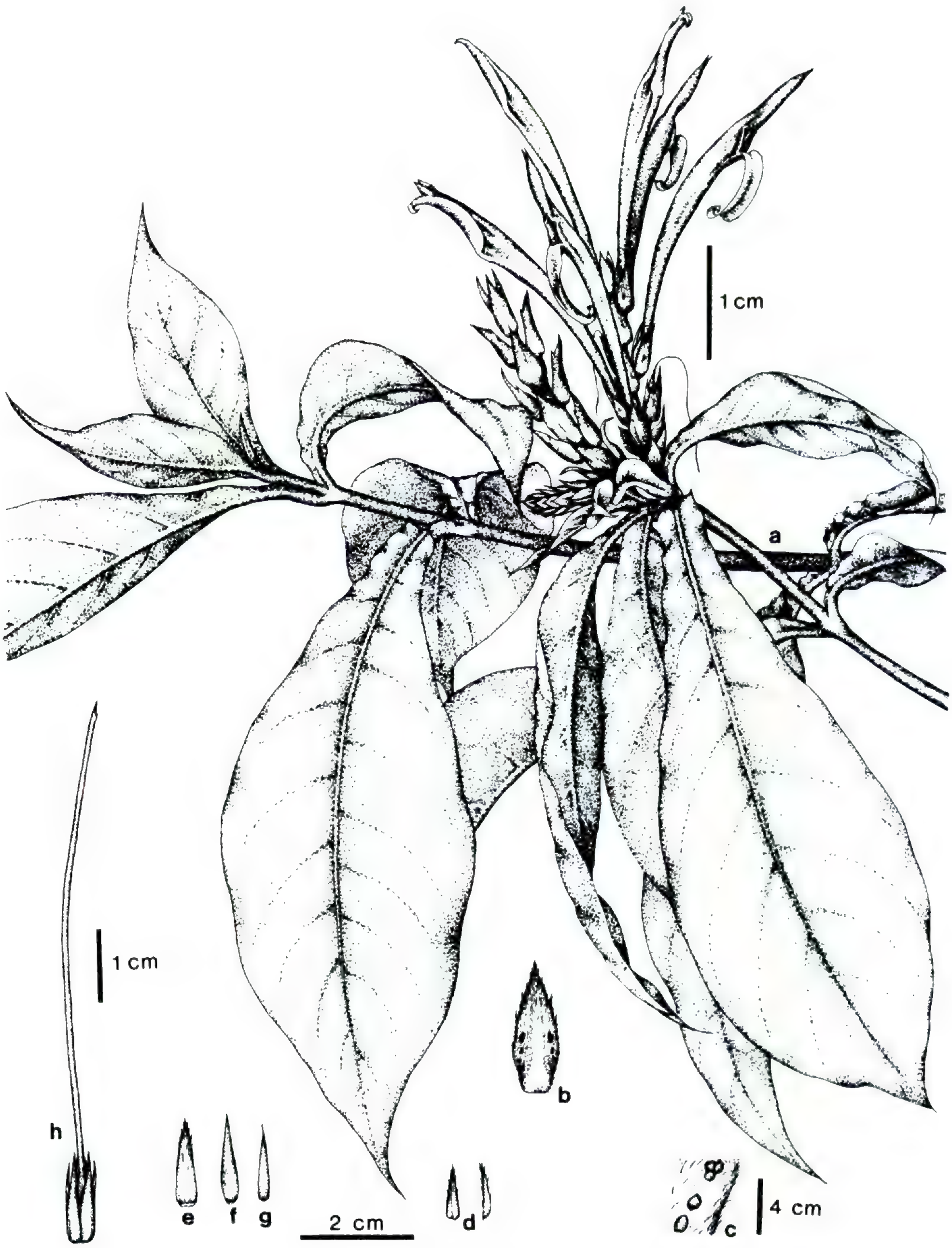


FIGURE 1. *Aphelandra panamensis* McDade, *McDade 388* (DUKE).—A. Distal portions of flowering and vegetative branches.—B. Floral bract.—C. Bracteal nectaries.—D. Bracteoles.—E. Adaxial sepal.—F. One of abaxial pair of sepals.—G. One of lateral pair of sepals.—H. Gynoecium with oblique stigma, filiform style, and ovary concealed by calyx.

spikes usually solitary (rarely to 5), terete, 4–12 cm long, 0.8–1.2 cm wide, sessile; the rachis densely pubescent, the trichomes erect, white, about 1 mm long; bracts slightly imbricate, narrowly rhombic-ovate, apically attenuate, marginally with 2–3 pairs of teeth (each 1–2 mm long), 11–15 mm long, 6–8 mm wide, green to pale dull orange, sparsely pubescent within, moderately pubescent without, the trichomes appressed, white, about 0.5 mm long, margins ciliate, the trichomes white, 0.25–0.5 mm long, the nectaries medial, composed of several (5–10) individual glands, each about 0.5 mm long and 0.3 mm wide; bracteoles lanceolate, apically acute, 6–10 mm long, 1.5–2.5 mm wide, straw-colored or green, glabrous except keel apically sparsely pubescent, the trichomes erect, white, about 0.75 mm long. Sepals 8–12 mm long, apically acute, green or straw-colored, glabrous except for the sparsely pubescent tip, the trichomes erect, white, about 0.75 mm long, the adaxial segment narrowly ovate, 3–5 mm wide, the abaxial pair lanceolate, 2–3 mm wide, the lateral pair narrowly lanceolate, 1.5–2 mm wide; corolla bright red, 5.5–7.0 cm long, minutely puberulous except tip of lower lip sparsely pubescent, the tube about 5 cm long, 2.5–3 mm in diameter at base, constricted to 1.5 mm above ovary (about 8 mm above base), expanding to 5–7 mm deep at throat, the upper lip erect, elliptic, 14–20 mm long, 6–8 mm wide, bilobed, the lobes triangular, acute, 5–7 mm long, anther pocket poorly developed, the middle lobe of lower lip narrowly elliptic, 18–23 mm long, 4–7 mm wide, acute, tip strongly curled back toward tube, the lateral lobes about 0.5 mm long and 3 mm wide; filaments inserted about 5 mm above base of tube, free portion of each about 5.0 cm long, the anthers 4–5 mm long, extending to within 2–3 mm of tip of upper lip, pollen very pale yellow; stigma not distinctively colored, oblique and appearing hollow, the style filiform, extending 1–2 mm beyond anthers, the ovary glabrous. Fruits globose, terete, glabrous, green tinged with orange when immature, becoming yellow-brown at dehiscence, 16–19 mm long, 4.5–6.5 mm wide, 5.5–7 mm thick; seeds dark brown, irregularly orbicular, slightly flattened, 4–6 mm in diameter, 2–3 mm thick. Seed germination semi-hypogeal.

Aphelandra panamensis is known only from central and eastern Panama in the provinces of Coclé, Colón, Panamá, San Blas and Darién. It occurs in wet cloud forest habitats, predominantly above 600 m elevation, but occasionally lower where local climatic conditions result in high rainfall and frequent fog cover. Individuals of this species are understory shrubs in primary and advanced secondary forest.

Peak flowering occurs in the wet season, from September to December, and fruits mature during the driest months of the year (late December to early March). There is, however, considerable asynchrony among individuals at some sites, notably the Santa Rita Ridge plants in the province of Colón where flowering individuals can be collected during most months.

The combination of toothed bracts with extrafloral nectaries, and the 5.5–7.0 cm long corolla serve to distinguish *A. panamensis* from other species of *Aphelandra*. Specimens of *A. panamensis* have previously been referred to *A. deppeana* (Wasshausen, 1975; Durkee, 1978) from which they may be readily distinguished by several morphological characters including habit, leaf vestiture, corolla length, and fruit size and color. The two species differ markedly in habitat and

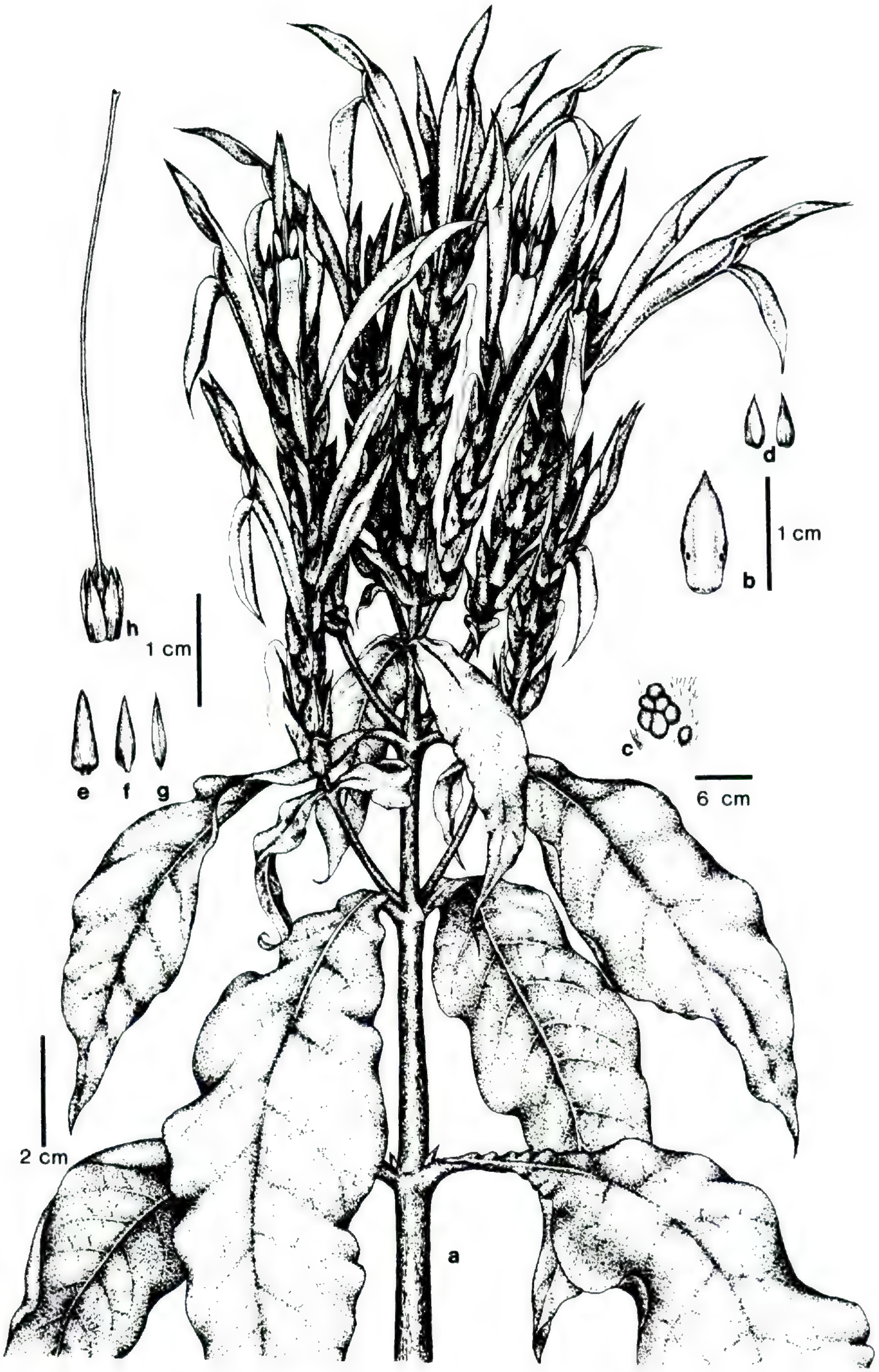
are wholly allopatric. The two-fold difference in corolla length is correlated with pollination by distinct animals. *Aphelandra panamensis* is pollinated by hummingbirds with long, decurved bills (Phaethorninae), while pollinators of *A. deppeana* are species with shorter, straight bills (Trochilinae) (McDade, 1980).

Additional specimens examined: PANAMA, COCLÉ: 8 km N of El Cope de Veraguas, near sawmill, 600–750 m elev., *Berg & Dressler 2770* (US). COLÓN: Ca. 7 mi from Transisthmian Hwy, Santa Rita Ridge, *Wilbur et al. 15078* (DUKE), *McDade 283, 388* (DUKE), *Smith & Smith 3433* (US). DARIÉN: S of El Real on slopes of Cerro Pirre, 500–1,000 m elev., *Foster & Kennedy 1263* (DUKE), *McDade 428* (DUKE). PANAMÁ: Cerro Jefe, about 8 km above Goofy Lake, 800 m elev., *Blum et al. 1834* (FSU), *Foster & Kennedy 1872* (DUKE, US), *Wilbur et al. 11316* (DUKE), *Lewis et al. 282* (DUKE, MO, US). SAN BLAS: Between Río Diablo and Río Acuati near Nargana, *Duke 14887* (US).

Aphelandra golfodulcensis McDade, sp. nov. TYPE: Costa Rica, San José, Vicinity of El General, beside Río Chirripó, *Skutch 2573* (MO, holotype; A, GH, NY, US, isotypes).—FIG. 2.

Frutex 1–6 m altus, foliis ellipticis vel oblanceolatis, 25–30(45) cm longis, 12–15 cm latis. Inflorescentiae spicatae, terminales, numerosae, 3–15 cm longae, 0.75–1 cm latae, pedunculus 0.5–10 cm longus; rachis minute puberula; bracteae imbricatae, rhombeo-ovatae, integrae, 8–13 mm longae, 4–7 mm latae, virides vel sordide aurantiacae, nectaria 1–7 glandibus, glandes singulae 0.75 mm longae, 0.5 mm latae; bracteolae anguste-ovatae, 4–6.5 mm longae, 2–4 mm latae, virides. Calycis lobi anguste-ovati vel lanceolati, 6–9 mm longi, 1.5–4 mm lati; corolla aurantiaca vel rubra, 6.3–7.3 cm longa, tubo 4.7 cm longo, labium superum 17–19 mm longum, 7–11 mm latum, lobus medius inferiores 22–26 mm longus, 6–9 mm latus; antherae 6–8 mm longae; stigma bilobum. Fructus immaturi virides, 19–23 mm longi, 5.5–7 mm lati, seminae atrobrunneae orbiculares, 4–6 mm in diam., 2.5–3 mm crassae. Germinatio semihypogaea.

Shrubs or small trees 1–6 m high, profusely branching; stems terete, younger stems densely pubescent, becoming moderate to sparse on older surfaces, the trichomes erect to downwardly appressed, white, about 0.75 mm long. Leaves opposite (rarely alternate), elliptic to oblanceolate, 25–30(–45) cm long, 12–15 cm wide, apically acute to acuminate (the tip acute or blunt), basally attenuate and decurrent on petiole, marginally entire or slightly undulate, upper surface essentially glabrous, sparsely pubescent on veins, the trichomes appressed, white, about 0.5 mm long, moderately pubescent below, the trichomes appressed (erect on veins), white, about 0.75 mm long; petioles to 1 cm long, moderately pubescent, the trichomes erect, white, about 0.5 mm long; leaves subtending inflorescences much reduced, 3–6 cm long, 1–2.5 cm wide, pubescence as of cauline leaves. Inflorescences terminal, spikes numerous, terete, 3–15 cm long, 0.75–1 cm wide, arranged in a freely branching paniculate inflorescence; the peduncles 0.5–10 cm long, moderately pubescent, the trichomes erect to downwardly appressed, white, about 0.75 mm long; the rachis minutely puberulous, the trichomes erect, white; bracts imbricate, rhombic-ovate, apically acute, entire, 8–13 mm long, 4–7 mm wide, green to dull brown-orange, glabrous to sparsely papillate within, minutely puberulous without, the trichomes appressed, white, margin ciliolate, the trichomes white, about 0.25 mm long, the nectaries submedial, composed of several (1–7) individual glands, each about 0.75 mm long and 0.5 mm wide; bracteoles narrowly ovate, apically attenuate, 4–6.5 mm long, 2–4 mm wide, green, moderately puberulous, the trichomes appressed, white. Sepals 6–9 mm long, apically acute, green, finely striate, minutely puberulous,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the trichomes appressed, white, the adaxial segment narrowly ovate, 3–4 mm wide, the abaxial pair broadly lanceolate, 2–2.5 mm wide, the lateral pair narrowly lanceolate, about 1.5 mm wide; corolla orange to red, 6.3–7.3 cm long, minutely puberulous, the trichomes erect, white, the tube about 4.7 cm long, 2–3 mm in diameter at base, slightly constricted above ovary (6 mm above base), expanding to 6–8 mm deep at throat, the upper lip erect, elliptic, 17–19 mm long, 7–11 mm wide, bilobed, the lobes triangular, acuminate, 6–10 mm long, anther pocket well-developed, the middle lobe of lower lip broadly lanceolate, 22–26 mm long, 6–9 mm wide, acuminate, the lateral lobes 1–3 mm long, 5–7 mm wide; filaments inserted about 15 mm above base of corolla tube, free portion of each about 4.0 cm long, the anthers 6–8 mm long, extending to within 5 mm from tip of upper lip, pollen very pale orange; stigma red, slightly bilobed, the lobes about 0.5 mm long, the style filiform, extending 3–5 mm beyond anthers, the ovary glabrous. Fruits clavate, terete, glabrous, green when immature, turning black brown at dehiscence, 19–23 mm long, 5–8 mm wide, 5.5–7 mm thick. Seeds dark-brown, orbicular, slightly flattened, 4–6 mm in diameter, 2.5–3 mm wide. Seed germination semi-hypogeal.

Aphelandra golfodulcensis is found primarily in the wet lowlands of the Golfo Dulce region of Puntarenas province, Costa Rica. Its range extends into the adjacent Burica Peninsula of Panamá (Chiriquí province), to mid-elevations above the Golfo Dulce region (provinces of Puntarenas and San José), and to the north into Alajuela and Guanacaste provinces where local conditions result in a more mesic and less seasonal climate than is typical of these areas. The plants occur as understory shrubs in primary and secondary forests, especially in edge habitats.

Peak flowering of *Aphelandra golfodulcensis* occurs during the dry season, from late December through March. Fruits mature rapidly and few individuals are still bearing fruits when the wet season begins in this area (mid April to early May).

Plants of this species have previously been referred to *A. sinclairiana* (Leonard, 1938; Wasshausen, 1975) from which they are readily distinguished morphologically. Especially distinctive are bract size, color, and pubescence; fruit color and pubescence; and overall vestiture of the plants. Individuals of *A. sinclairiana* have bright orange bracts 16–20 mm in length, black, pubescent fruits, and erect, pilose pubescence of stems, leaves, bracts and corollas.

Additional specimens examined: COSTA RICA, ALAJUELA: Vicinity of Capulín on Río Grande de Tárcoles, 80 m elev., *Standley 40160* (US); Santiago de San Ramón, *Brenes 6625* (A, F, NY). GUANACASTE: El Arenal, *Standley & Valerio 45105* (US). PUNTARENAS: Ca. 10 km SE (toward Panamá) of Palmar N along InterAmerican Hwy, *Burger & Matta-U. 4646* (F, MO, NY), *McDade 378* (DUKE); Esquinas forest, between Río Esquinas and Palmar Sur, *Allen 5775* (F, GH, US); Golfo Dulce and

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FIGURE 2. *Aphelandra golfodulcensis* McDade, *McDade 251* (DUKE).—A. Tip of flowering branch.—B. Floral bract.—C. Bracteal nectaries.—D. Bracteoles.—E. Adaxial sepal.—F. One of abaxial pair of sepals.—G. One of lateral pair of sepals.—H. Gynoecium with bilobed stigma, filiform style, and ovary concealed by calyx.

Río Térraba, *Skutch 5406* (F, US); forests of Santo Domingo de Golfo Dulce, *Tonduz 9969* (NY, US); Rincón de Osa, *Burger & Gentry 8851* (F); Sirena, Corcovado National Park, sea level, *McDade 401* (DUKE); Cañas Gordas, *Pittier 11193* (US); ca. 5 mi from San Vito de Java, Las Cruces Botanical Garden, *McDade 395* (DUKE). SAN JOSÉ: Río Pacuar, vicinity of El General, *Skutch 3941* (MO, NY, US); Río Chirripó del Pacifico between Canaán and Chimiról, *Burger & Liesner 7117* (F, MO). PANAMA, CHIRIQUÍ: Pto. Armuelles, 1 mi W of airport, *Croat 21884* (F, MO, NY); ca. 2 mi S of Pto. Armuelles, *Wilbur et al. 13583* (DUKE, F); San Bartolo Limite near Costa Rican border, 12 mi W of Pto. Armuelles, 400–500 m elev., *Croat 22194* (DUKE, MO).

Aphelandra leonardii McDade, sp. nov. TYPE: Panama, Panamá: Majé, about 5 mi up Río Nuevo, a branch of Río Majé, *Foster & Kennedy 1993* (DUKE, holotype; F, MO, isotypes).—FIG. 3.

Frutex 1–5 m altus, foliis oblanceolatis vel ellipticis, 10–20(–30) cm longis, 4–10 cm latis. Inflorescentiae spicatae, terminales, una vel numerosae, sessiles, quadrangulares, 3.5–14 cm longae, 0.8–1 cm latae; rachis sparsim pubescens; bracteae vix imbricatae, rhombeo-ovatae, integrae, 7–10 mm longae, 5–7 mm latae, virides vel aurantiacae, nectaria 2–3 mm longa, 1–2 mm lata, glandibus numerosis et minutis munita; bracteolae lanceolatae, 6–9 mm longae, 2–3 mm latae, virides. Calycis lobi anguste-ovati vel lanceolati, 10–12 mm longi, 1.5–5 mm lati, luteo-virides; corolla rubra, 6–7.3 cm longa, tubo 5 cm longo, labium superum 17–21 mm longum, 8–10 mm latum, lobus medius inferiores 21–28 mm longus, 8–10 mm latus; antherae 7–8 mm longae; stigma bilobum. Fructus immaturi virides 17.5–19 mm longi, 5 mm lati, 3.5–4 mm crassi; seminae brunneae, orbiculares, complanatae, 3.5–6.5 mm in diam., 1.5–2 mm crassae. Germinatio epigaea.

Shrubs 1–5 m high, profusely branching; younger stems quadrangular, sparsely pubescent, the trichomes upwardly appressed, white, about 0.5 mm long, older stems terete, glabrate. Leaves opposite, obovate to elliptic, 10–20(–30) cm long, 4–10 cm wide, apically acuminate, basally acute to attenuate, marginally entire to slightly undulate, upper surface glabrous, lower surface glabrous to sparsely pubescent except veins sparsely to densely pubescent, the trichomes appressed, white, 0.5–0.75 mm long; petioles 0.3–1.5 cm long (rarely to 3 cm), sparsely pubescent, the trichomes appressed, white, about 0.5 mm long. Inflorescence terminal, spikes solitary to numerous, quadrangular, 3.5–14 cm long, 0.8–1.0 cm wide, sessile or rarely very short pedunculate; rachis sparsely pubescent, except frequently densely pubescent just below insertion point of each bract, the trichomes erect, white, about 0.5 mm long; 2–3 pairs of imbricate, densely pubescent sterile bracts borne below fertile bracts, the trichomes appressed, white, about 0.75 mm long; floral bracts barely imbricate, rhombic-ovate, apically acute, marginally entire, 7–10 mm long, 5–7 mm wide, green to bright orange, glabrous within, sparsely and minutely puberulous without, margin minutely ciliolate, the trichomes white, the nectaries sub-medial, 2–3 mm long and 1–2 mm wide, composed of many minute glands (each ca. 0.1 mm in diameter); bracteoles lanceolate, apically attenuate, 6–9 mm long, 2–3 mm wide, green, finely striate, glabrous except densely pubescent on keel, the trichomes erect, white, about 0.5 mm long.

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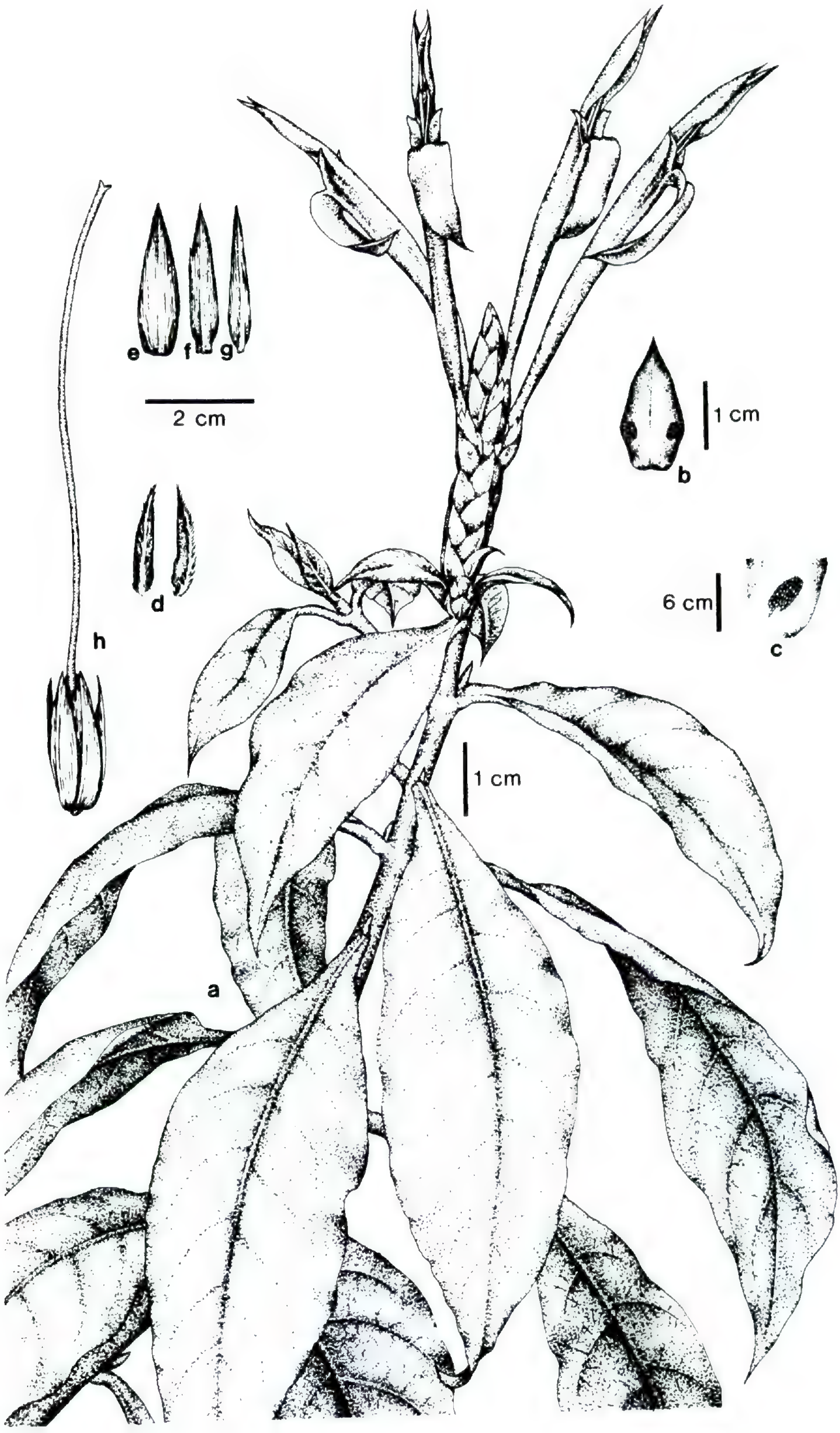
FIGURE 3. *Aphelandra leonardii* McDade, *McDade 310* (DUKE).—A. Tip of flowering branch.—B. Floral bract. —C. Bracteal nectary patch.—D. Bracteoles.—E. Adaxial sepal.—F. One of abaxial pair of sepals.—G. One of lateral pair of sepals.—H. Gynoecium with minutely bilobed stigma, filiform style, and ovary concealed by calyx.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Sepals 10–12 mm long, apically acute, yellow-green, finely striate, margins hyaline, essentially glabrous, the adaxial segment narrowly ovate, 3–5 mm wide, the abaxial pair lanceolate, about 3 mm wide, the lateral pair narrowly lanceolate, 1.5–2 mm wide; corolla bright red, 6–7.3 cm long, essentially glabrous, the tube about 5 cm long, 4–5 mm in diameter at base, constricted to 1.5–2 mm above ovary (about 7 mm above base), expanding to 7–9 mm deep at throat, the upper lip erect, elliptic, 17–21 mm long, 8–10 mm wide, bilobed, the lobes triangular, acute and apiculate, 9–10 mm long, anther pocket well-developed, the middle lobe of lower lip narrowly ovate, strongly reflexed to lie along tube at anthesis, 21–28 mm long, 8–10 mm wide, acute, apiculate, the lateral lobes about 1 mm long and 6 mm wide; filaments inserted 8–11 mm from base of tube, free portion of each 4.5–5.3 cm long, the anthers 7–8 mm long, extending to within 4–6 mm from tip of upper lip, pollen yellow; stigma not distinctively colored, slightly bilobed, the lobes about 0.2 mm long, the style filiform, extending 1–6 mm beyond anthers, the ovary glabrous. Fruits oblong, flattened, oval in cross section, glabrous, yellow-green when immature, yellow-brown at dehiscence, 17.5–19 mm long, about 5 mm wide, 3.5–4 mm thick; seeds brown, irregularly orbicular, strongly flattened, 3.5–6.5 mm in diameter, 1.5–2 mm thick. Seed germination epigeal.

This species is known from lowland and premontane forests in eastern Panamá (Colón, Panamá, Darién, and San Blas), and from two localities in Costa Rica. Extensive collecting on the Caribbean slope of Panamá will be required to firmly establish the range of this species. *Aphelandra leonardii* is a shrub of the forest understory and margins. Plants of this species are found in areas with little annual variation in rainfall, but a few collections have been made in seasonally dry regions.

Aphelandra leonardii flowers during the late wet season (September to December), and fruits mature during the driest months of the year (January to April).

Individuals of this species may be distinguished from other Central American members of the *A. pulcherrima* complex by the combination of shrubby habit, sessile, terminal clusters of inflorescences, and small, rhombic-ovate, entire floral bracts. Specimens of this new species were formerly referred to *A. pulcherrima* H.B.K. (Wasshausen, 1975; Durkee, 1978) from which they differ most notably in the morphology of the bracteal nectaries. In *A. pulcherrima* the glands are few and large, whereas in *A. leonardii,* they are numerous, minute, and form a well-defined oblong patch on each side of the bract. The two species also differ in fruit and seed morphology, with terete capsules and sub-globose seeds present in *A. pulcherrima,* and strongly flattened capsules and seeds present in *A. leonardii*. *Aphelandra pulcherrima* is wholly South American and appears to include at least three closely related species (contrast, for instance, the treatments of Leonard, 1953, and Wasshausen, 1975).

While there is little morphological variability among the eastern Panamanian plants of this species, individuals from Costa Rica are rather distinct in several features of vegetative morphology. Costa Rican plants are larger and more diffusely branched, and have leaves that are membranous, narrower (3–5 cm), and sparsely pubescent. With respect to inflorescences and flower characters, however, plants from the two regions are extremely similar. The systematic signifi-

cance of the differences is as yet unclear and will hopefully be clarified by further collections in intervening areas from which the species is yet unknown. While it is possible that collections from the two countries represent distinct species, data from interpopulation crosses (McDade, 1980) support recognition of a single species.

The specific epithet honors E. C. Leonard, in recognition of his many valuable contributions to knowledge of Neotropical Acanthaceae.

Additional specimens examined: COSTA RICA, SAN JOSÉ: Along Río Tarrazú between Frailes and San Andrés, 1,300 m elev., *Burger 4041* (DUKE, F, MO, NY), *McDade 310* (DUKE). PROVINCE unknown: Near Boca Culebra, Pacific coast (Puntarenas?), *Pittier 11988* (US). PANAMA, COLÓN: Forest along Río Indio de Gatun, sea level, *Maxon 4807* (NY, US); Río Providencia, 3 km SE of Achiote, 5–100 m elev., *Gentry & Nee 8652* (MO); Río Guanche, *D'Arcy 9696* (MO). DARIÉN: Slopes of Cerro Pirre, 500–2,500 ft elev., *Duke & Elias E13889* (MO); summit camp between Sasardí and Mortí, 400 m elev., *Duke 10033* (MO); summit camp adjacent Darién-San Blas border along sea level canal route 17, 1,000–1,200 ft elev., *Oliver et al. 3676* (MO, US); between upper Río Membrillo and Camp 7 on construction road to San Blas, *Duke 10865* (NY); Río Tucutí between Tucutí and Río Urogantí, *Duke 5287* (MO); Río Aruza, *Bristan 1248* (MO). PANAMÁ: Along Río Chavaré above Chepo, 50–200 m elev., *Pittier 4723* (US); along InterAmerican Hwy between El Llano and Río Mamoní, *Duke 5631* (MO). SAN BLAS: Along beach east of Pto. Obaldía, *Croat 16890* (US); forest around Pto. Obaldía, *Pittier 4280* (GH, NY, US); mainland opposite Ailigandí from mouth of Ailigandí River, *Lewis et al. 172* (DUKE, MO, NY, US).

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XYRIS APUREANA KRAL & SMITH, A NEW SPECIES OF *XYRIS* (SECT. *NEMATOPIS*) FROM VENEZUELA[1]

ROBERT KRAL[2] AND LYMAN B. SMITH[3]

Xyris apureana Kral & Smith, sp. nov.—TYPE: VENEZUELA, APURE, Distrito Pedro Camejo, ca. 2 km S of Caño La Cochina de La Pica along the main road south of Paso de San Pablo to the Río Cinaruco, 6°42′N, 67°48′W, elev. 70 m, morichal and surrounding marshy grassland, 2 March 1979, *G. Davidse & A. C. Gonzalez 15948* (US, holotype; MO, VDB, VEN, isotypes).—FIG. 1.

Herba perennis, laxa, densicaespitosa, glabra. Rhizomata tenuia, brevia vel elongata, ascendentia. Radices graciles. Folia linearia, 1.5–3.0 dm longa, erecta vel leviter expansa, subdisticha, vaginis scaporum longiora. Laminae vaginis 5–10-plo longiores, 1–2 mm latae, planae, rectae, longitudine pauci-pluri-costatae et sulcatae, a basi ad medium compressae, apicem versus teretes vel subteretes, apices contracti, angusti rotundati, incrassati, persaepe canaliculati, margines integri, non incrassati; vaginae carinatae, pallide lamprobrunneolae, pluricostatae, praeter costas scariosae, marginibus in laminas gradatim convergentibus, ad apicem ligulam scariosam curtam latam fascientibus, infime gradatim expansae, acies integrae. Vaginae scaporum laxae, tortae, multicostatae, ad apicem dilatatae; laminae breves, rectae. Scapi graciles, teretes, recti vel aliquantum flexuosi, 2.5–3.5 dm alti, 0.5–0.6 mm crassi, olivacei vel rubelli. Spicae pluriflorae, ellipticae, 5–6 mm longae, acutae, bracteae subdecussatae, naviculares vel convexae, ecarinatae sed mediane 1-nervosae, scariosae, ferrugineae, erosae; bracteae steriles 4, pari infimo oblongo saltem medium spicae aequans, pari intimo ovato ca. 3 mm longo; bracteae fertiles ovatae usque ad 4 mm longae; area dorsali lanceolata, ferruginea vel brunneola, bractearum dimidium vel totum aequans. Sepala lateralia lanceolata, valde inequilatera, ca. 4 mm longa, acuta; ala carinali angusta sed fortes, integra. Laminae petalorum late obovatae, 2.5–3.0 mm longae, late rotundatae, valde erosae, cuneatae, luteolae. Staminodia bibrachiata, brachiis longipenicellatis. Antherae oblongae, ca. 1.5 mm longae, retusae et sagittatae, filamentis parum longiora. Capsula oblonga, planoconvexa, placenta basalia. Semina anguste oblonga, persaepe curvata, ca. 1 mm longa, translucida, ferruginea, longitudine leviter multicostata.

Perennial, lax, densely caespitose, smooth herb. Rhizomes slender, short to elongate, ascending (this may have to do with degree of depth in substrate!). Roots slender. Leaves linear, 1.5–3.0 dm long, erect or slightly spreading, subdistichous, longer than the scape sheaths; blades 5–10 times longer than the sheaths, 1–2 mm wide, flat, straight, longitudinally few-to-many-costate and sulcate, from base to middle flattened, toward the apex terete or subterete, the apices narrowed, narrowly rounded, thickened, often channelled, the margins entire, not thickened; sheaths carinate, pale shining brown, several nerved, except for the ribs scarious, the margins gradually converging into the blades, at the apex producing a short, broad, scarious ligule, below gradually expanding, the edges entire. Scape sheaths lax, twisted, multicostate, at the apex dilated; blades short, erect. Scapes slender, terete, straight or somewhat flexuous, 2.5–3.5 dm high, 0.5–0.6 mm thick, olivaceous to reddish. Spikes several-flowered, elliptic, 5–6 mm long, acute, the bracts subdecussate, navicular or convex, ecarinate but medially 1-nerved, scarious, ferrugineous, erose; sterile bracts 4, the lowest pair at least half as long as

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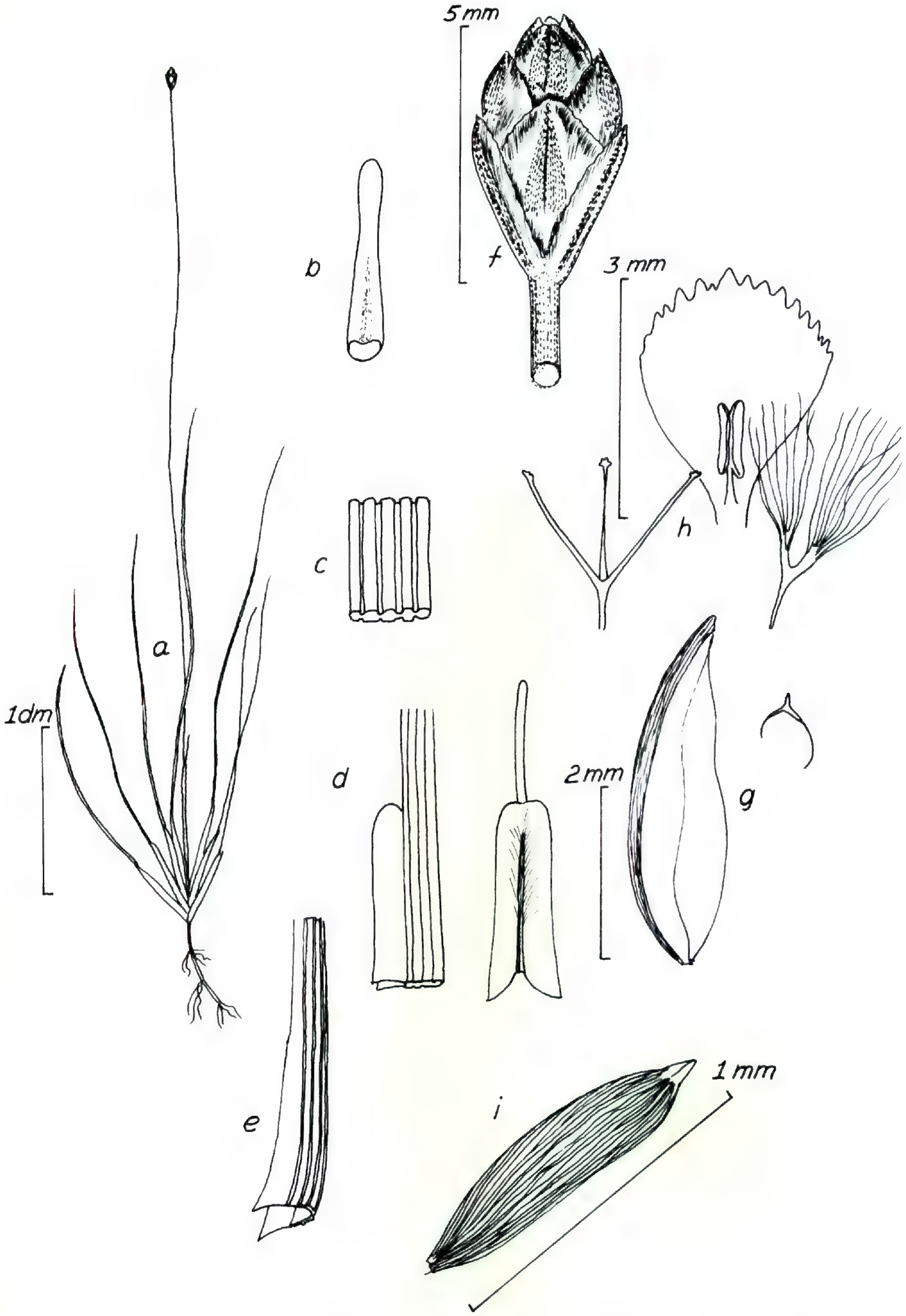

FIGURE 1. *Xyris apureana* Kral & Smith (from *Davidse & Gonzalez 15984*). a. habit sketch, b. leaf apex, c. sector of mid-blade, d. junction of sheath and blade, e. leaf sheath base, f. spike, g. lateral sepal, h. petal blade and stamen, stylar apex, staminode, i. seed.

the spike, oblong, the inner pair ovate, ca. 3 mm long; fertile bracts ovate, to 4 mm long; dorsal area lanceolate, reddish-brown or brownish, half as long as or equal to the bract. Lateral sepals lanceolate, strongly inequilateral, ca. 4 mm long, acute; carinal keel narrow but strong, entire. Petal blades broadly obovate, 2.5–3.0 mm long, broadly rounded, strongly erose, cuneate, yellowish. Staminodes bibrachiate, the branches long-penicillate. Anthers oblong, ca. 1.5 mm long, retuse and sagittate, slightly longer than the filaments. Capsule oblong, planoconvex, placentation basal. Seeds narrowly oblong, often curved, ca. 1 mm long, translucent, ferrugineous, longitudinally finely multicostate.

Due to its flattened leaves, *Xyris apureana* comes to 55. *X. rubrolimbata* in the key to *Xyris* species of the Guayana Highland (Maguire & Smith, 1964), but differs greatly in habit.

If this smooth, elongate-rhizomed, soft-foliaged plant had terete leaves it would bear a strong resemblance to *X. aquatica*, *X. terrestris*, and *X. juncifolia*. The scarious sheath apex (ligular area) is distinctly broader than is the leaf base, but the ligule is adnate nearly to its apex; the keel of the lateral sepal is absolutely entire.

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XYRIS NIGRESCENS KRAL, A NEW SPECIES OF *XYRIS* (SECT. *NEMATOPUS*) FROM COSTA RICA[1]

ROBERT KRAL[2]

In the preparation of a treatment of Xyridaceae for the Americas north of South America I have examined specimens of a *Nematopus* from the highlands of Costa Rica that are similar to *Xyris subulata* R. & P. and its relatives but that are distinct enough in several characters to warrant description as a new species:

Xyris nigrescens Kral, sp. nov. TYPE: COSTA RICA, SAN JOSÉ, Laguna de la Chonta northeast Santa Maria de Dota, 18 Dec. 1925, *P. C. Standley 42329*. US, holotype; *P. C. Standley 42131* (US, topotype).—FIG. 1.

Planta perennis, densicaespitosa. Radices graciles. Folia rigida, erecta, linearia, solum basalia, 1.5–8.0 dm longa, vaginis scaporum longiora; laminae vaginis 10–15-plo longiores, planae vel tortae, 2.5–4.5 mm latae, flavovirentae, valde compressae, longitudine leviter multinervosae, apices contracti, incurvato-acuti, incrassati, margines incrassati, persaepe papillosi; vaginae leviter carinatae, carinibus interdum ferrugineociliatis, lateribus glabris, brunneolis, nitidis, marginibus tenuibus integris vel basin versus ciliatis, in laminas gradatim convergentibus sed ad apicem ligulam triangulam 2.0–2.5 mm longam efferentes. Vaginae scaporum basin versus leviter compressae, laxae, brunneolae, nitidae; laminae breves, cuspidatae. Scapi lineares, recti, leviter torti, 5–7 dm alti, 1–2 mm lati, virides, apicem versus ancipiti, in sectione transversali elliptici, bicostati, costis papillosis. Spicae subcapitatae, pluriflorae, ca. 1 cm longae, 1 cm latae, bracteae ecarinatae, convexae, fuscae; bracteae steriles 6–7, ovatae, fertilibus breviores; bracteae fertiles laxe imbricatae, ovatae vel anguste ovatae, ca. 5 mm longae, integrae vel laceratae, tenues; area dorsali nulla. Sepala lateralia libera, fusca, inequilatera, leviter curvata, oblanceolata, ca. 5 mm longa, acuta; ala carinali firma, angusta, integra vel apicem versus ciliata. Laminae petalorum anguste obovatae, ca. 5 mm longae, apice rotundatae, erosae, cueatae, luteolae. Staminodia bibrachiata, brachiis apice sparsim longipenicillatis. Capsula ellipsoidea, 5 mm longa, placenta centralis. Semina oblonga, 0.8–1.0 mm longa, translucida, atroferruginea, 16–20-costata.

Caespitose perennial. Roots slender. Leaves stiffish, erect, linear, strictly basal, 1.5–8.0 dm long, longer than the scape sheaths; blades 10–15 times longer than the sheaths, flat or twisted, 2.5–4.5 mm wide, yellow green, strongly flattened, longitudinally finely multinerved, the apices narrowed, strongly incurved-acute, thickened, the margins incrassate, often papillose; sheaths somewhat carinate, the carinas sometimes reddish brown-ciliate, the sides smooth, brownish, shining, the margins thin, entire or toward base ciliate, gradually converging into the blades but at the apex developing a triangular ligule 2.0–2.5 mm long. Sheaths of scapes somewhat compressed toward the base, loose, brownish, lustrous, with the blades short, cuspidate. Scapes linear, erect, slightly twisted, 5–7 dm high, 1–2 mm wide, green, ancipital toward the apex, in cross section elliptical, bicostate, the costas papillose. Spikes subcapitate, several-flowered, ca. 1 cm long, 1 cm wide, the bracts ecarinate, convex, dark brown; sterile bracts 6–7, ovate, shorter than the fertile; fertile bracts loosely imbricate, ovate or narrowly ovate,

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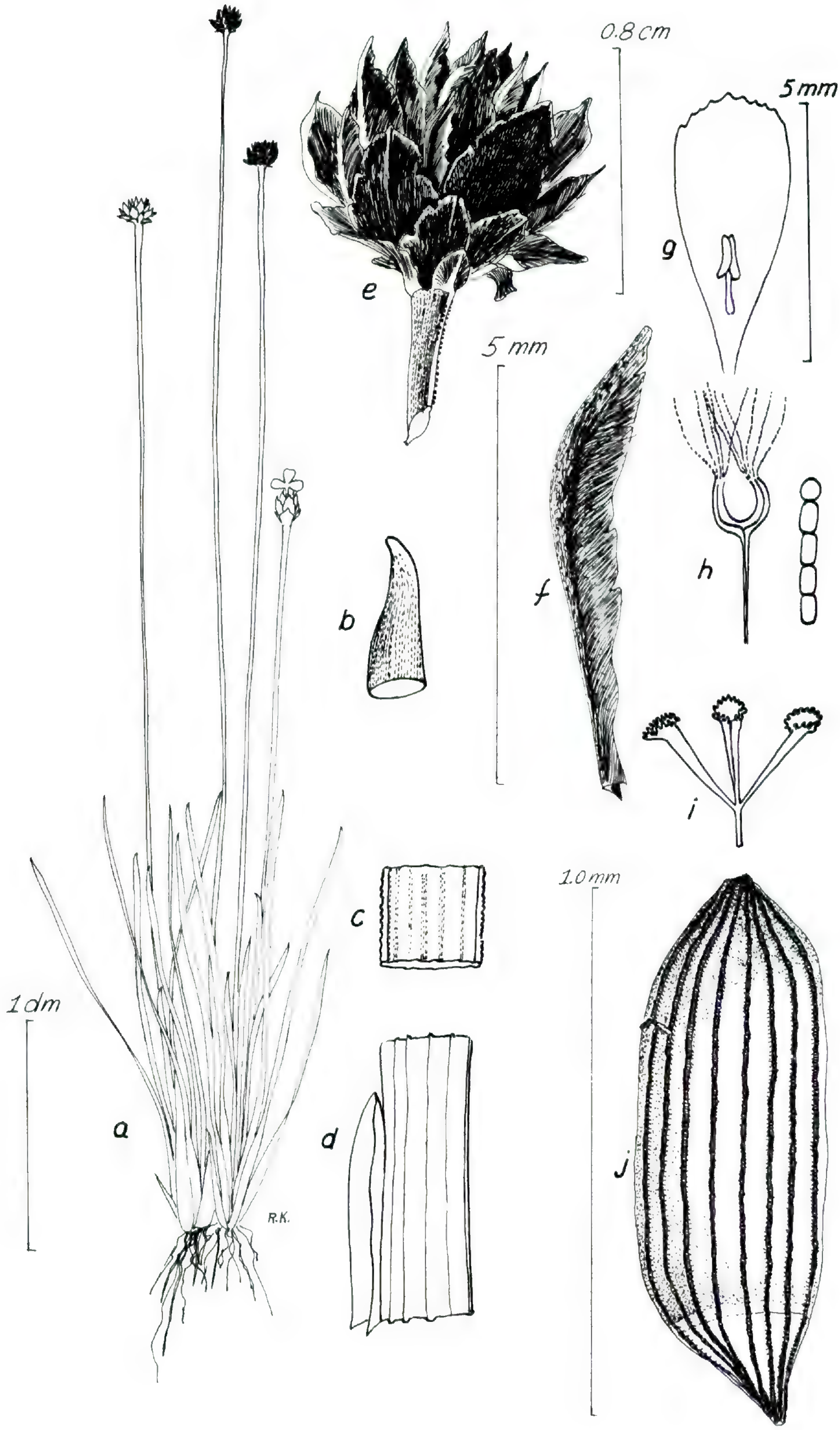
0.8 cm
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ca. 5 mm long, entire or (with age) lacerate, thin; dorsal areas none. Lateral sepals free, dark brown, inequilateral, slightly curvate, oblanceolate, ca. 5 mm long, acute; keel firm, narrow, entire or ciliate toward the apex. Petal blades yellowish, narrowly obovate, ca. 5 mm long, apically rounded, erose, the base cuneate. Staminodia bibrachiate, the branches apically long-penicillate. Capsule ellipsoidal, 5 mm long, the placenta central. Seeds oblong, 0.8–1.0 mm long, translucent, dark reddish brown, 16–20-ribbed.

Additional material: COSTA RICA, CARTAGO: En terreno cenagoso, al sol, un poco al sur de El Empalme, en el llamado "Parque Vicente Lachner," 2,250 m, 17 Mayo 1964, *Alfonso Jiminez M. 1976* (F! US!).

This nematopoid *Xyris*, evidently related to *X. subulata* R. & P. and *X. weberi* H. J. Conert in its narrow but flattish leaves, its dark brown, loosely imbricated, thinnish, ecarinate bracts, differs from both in its broader, less twisted leaf blades, its longer ligules, and most markedly in the more floriferous, subcapitate spike. As is the case with the other species of this complex, *X. nigrescens* appears to be confined to high mountain bogs.

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FIGURE 1. *Xyris nigrescens* Kral (from *P. C. Standley 43239*). a. habit sketch, b. leaf apex, c. section of mid-blade, d. blade at junction with sheath; ligule, e. spike, f. lateral sepal, g. petal blade, h. staminode, i. style branches and stigmas, j. seed.

CHROMOSOME NUMBER OF *BYBLIS LINIFLORA* SALISB. (BYBLIDACEAE)[1]

CHING-I PENG[2] AND ANN KENTON[3]

ABSTRACT

Cytological studies of plants from two different sources cultivated at Missouri Botanical Garden, St. Louis and the Royal Botanic Gardens, Kew, suggest that *Byblis liniflora* Salisb. has a gametic chromosome number of $n = 16$ instead of $n = 12$ as reported by Kondo (1973). This previous and apparently erroneous report was cited in recent reviews of angiosperm chromosome numbers by Raven (1975) and Lewis (1980).

The carnivorous plant genus *Byblis* comprises 2 species: *B. gigantea* Lindl., a self-incompatible, moderately woody herb endemic to ephemeral swamps along sandy coastal plains in Western Australia (Morcombe, 1968), and *B. liniflora* Salisb., a smaller, self-compatible herb that is widespread across tropical Australia and that has recently been recorded in southern New Guinea (Steenis, 1968). The first chromosome count for this genus was made by Kress (1970), who reported $2n = 18$ for *B. gigantea*. Later Kondo (1973) reported a different number, $2n = 14$ for this species. In addition he reported $2n = 24$ for *B. liniflora*.

The discrepancy in the reported number for *Byblis gigantea* and the large difference in chromosome numbers between the two closely related species inspired us to reexamine these taxa using plant materials that are available in our respective institutions. We do not have access to plants of *B. gigantea*, but we do have cultivated plants of *B. liniflora* from two different sources. The plants at Missouri Botanical Garden were grown from seeds received from Ms. Patrick Dwyer, St. Michael's Episcopal Church, Killean Park, Albany, New York (MO accession number: 791501). The plants at the Royal Botanic Gardens, Kew, were grown from seeds obtained from the Insectivorous Society of Japan, and the stock originated from Western Australia (K accession number: 437-79-04433). Voucher specimens (*Solomon 5668* and *437-79-04433*) are preserved at MO and K respectively.

Meiotic counts prepared at Missouri Botanical Garden clearly show a haploid chromosome number of $n = 16$ (Fig. 1). Numerous good cells were observed, and meiosis was regular in both diakinesis and metaphase I. Mitotic counts made at the Royal Botanic Gardens yielded a diploid number of $2n = 32$ (Fig. 2). Our results are at variance with those reported by Kondo (1973) who received fixed root tips from plants grown by Mr. Joseph A. Mazrimas, Livermore, California. Initially we suspected the possibility of misidentification of these collections. However, photographs kindly sent by Mr. Mazrimas show that his plants were

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[1] We are grateful to P. H. Raven for communicating with Mr. Joseph A. Mazrimas, locating Kondo's original paper and making valuable comments on the manuscript. We also thank P. Goldblatt and P. P. Lowry for critically reading the manuscript, and Mr. D. Bowling for growing *B. liniflora* in sterile culture at Kew. Permission to cite unpublished work by G. J. Keighery is greatly appreciated.

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FIGURES 1 & 2. Chromosomes of *Byblis liniflora* Salisb.—1. Meiotic metaphase I, $n = 16$.—2. Mitotic metaphase, $2n = 32$. Calibration bar = 10 μm.

indeed of *B. liniflora* and *B. gigantea*, although the materials are no longer in cultivation nor are seeds still available.

It is of interest to note that $2n = 14$, the chromosome number reported by Kondo (1973) for *B. gigantea*, differs not only from an earlier report by Kress (1970) but also from a recent study by Keighery at Kings Park and Botanic Garden, West Perth, Western Australia (pers. comm.). Keighery traced the source of Kondo's seeds, and plants obtained from this area (Cannington, Australia) gave a count of $2n = 18$. In addition, the 27 plants Keighery examined (obtained from 7 populations sampled over the entire distribution range of *B. gigantea*) consistently exhibited a meiotic number of $n = 9$, an observation which is in agreement with that of Kress (1970).

Therefore, it seems possible that some confusion took place between the time the root tips were fixed and the chromosomes were counted by Kondo. However, it is also likely that Kondo simply misinterpreted his preparations. In our study, we noted that in some mitotic cells chromosomes were prone to aggregate together. This may be due to the fact that ends of the somatic chromosomes are very heterochromatic (Fig. 2), which would tend to cause stickiness. Thus it is likely that some of the "long" chromosomes that Kondo showed in his drawing for *B. liniflora* could actually be aggregates of 2 or 3 chromosomes, thus giving an apparent lower count.

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PRELIMINARY REPORT ON THE FLORA PROJECT OF LA SELVA FIELD STATION, COSTA RICA[1]

BARRY E. HAMMEL[2] AND MICHAEL H. GRAYUM[3]

ABSTRACT

Finca La Selva is an intensively studied biological field station with a poorly known flora. Presently we can account for about 1,500 species of vascular plants but the flora may contain as many as 2,000. Although collecting has been nearly continuous since the beginning of the project in the summer of 1979, we are still finding novelties. Experience at La Selva has driven home the fact that certain genera of both bulky and inaccessible plants have been habitually ignored by botanical collectors in the tropics. The wet Caribbean lowlands of Central America have themselves been relatively inaccessible and ignored. General collecting throughout the region is urgently needed.

HISTORY

Finca La Selva is a 730 hectare[4] biological field station owned and operated by the Organization for Tropical Studies (OTS), which is a consortium of North and Central American universities. The station is located near the confluence of the Puerto Viejo and Sarapiquí rivers in the province of Heredia in the Caribbean lowlands of northeastern Costa Rica. The property encompasses about 650 hectares of primary forest in addition to 80 hectares of disturbed land, including old pasture, abandoned cacao and pejibaye (peach palm) plantations, 25-year-old successional woods, and regularly maintained one- through five-year-old successional plots. In the Holdridge Life Zone system, the vegetation is classified as Tropical Premontane Wet Forest (Holdridge et al., 1971). The average annual rainfall is about 3,900 mm. The elevation varies from 100 m along the Rio Puerto Viejo on the north edge of the property to 220 m in the ridge-dissected southern section (Petriceks, 1956). Thus, the altitudinal range from one end of the property to the other, a distance of about 3.4 km, exceeds that from the Caribbean coast to the La Selva field station, a distance of about 55 km.

For the last 12 years the station has been the annual site of as many as three OTS courses in tropical ecology as well as a number of courses offered by other institutions. The site has served almost continuously for the last 25 years as base for many researchers and has been particularly attractive to plant ecologists. A bibliography of published papers based on work done at La Selva contained about 200 entries by fall of 1981. Nevertheless, until recently fewer than half the species of vascular plants now known to occur at the station had been even tentatively identified or otherwise accounted for.

The need for a means to identify plants at La Selva has been ever-present. Standley's Flora of Costa Rica (1937–1938) is much out of date and provides only

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[3] Department of Botany, University of Massachusetts, Amherst, Massachusetts 01003.

[4] The recently acquired and unexplored Vargas property nearly doubles the size of the station. It contains approximately equal areas of primary forest, secondary forest, and pasture.

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an annotated list for most groups. Even the last more detailed part is inadequate for our area; it treats, for example, only 20 of the 32 species of *Psychotria* (Rubiaceae) known for La Selva. The Flora of Panama, published in the Annals of the Missouri Botanical Garden from 1943 to the present, and now completed, has been the most useful reference. However, most of the earlier treatments and many recent ones are nearly obsolete (Dressler, 1972; Gentry, 1978). Standley's treatment of the Araceae (1944) lists 31 species of *Anthurium* (taking synonymy into account), whereas over 150 are known from Panama today. The same treatment lists 12 species of *Philodendron*; there are over 75 known to date (T. B. Croat, personal communication). More than twice as many species of *Monstera*, *Syngonium*, and *Philodendron* are known from La Selva alone than were observed for all of Panama in 1944. For pteridophytes the situation is even more grim; only the excellent reference collection maintained by Luis Diego Gómez at the Museo Nacional in San José is of any help.

Support to initiate the Flora of La Selva project was obtained in 1979 from the U.S. National Science Foundation (NSF/DEB 79-04417). Since that time, intensive collecting by Jim Folsom (University of Texas), Michael Grayum (University of Massachusetts), Barry Hammel (Duke), John MacDougal (Duke), Damon Smith (Duke), John Sperry (Duke), Carol Todzia (University of Texas) and Robert L. Wilbur (Duke) has led to the accumulation of more than 10,000 collections. All unicates remain at Duke University, and replicates will be distributed among the Field Museum, Museo Nacional de Costa Rica, and the Missouri Botanical Garden. We are also maintaining a reference collection at La Selva. This on-site herbarium is essential during the collecting period and will be an aid to future users of the station for making final determinations, especially of sterile material.

Although a full-scale national Flora of Costa Rica is in progress (Burger, 1971) the Flora of La Selva is in no way redundant. The two projects are complementary and quite different. The fascicles of the Flora Costaricensis are an immense help to our work at La Selva. At the same time the thousands of specimens coming out of La Selva will help fill the extensive gap in knowledge of the flora of Costa Rica's Caribbean lowlands.

Current Work

Based on these and previous collections (ca. 2,000), particularly those of Gary Hartshorn (Tropical Science Center, Costa Rica) and Paul Opler (U.S. Department of the Interior), we are maintaining a card catalogue of taxa known from La Selva. At the beginning of the project the available checklist contained only 710 species. Up to the fall of 1980 the list was still growing at an average rate of about one new species per day. To date first approximation identifications have been made for about 850 of the estimated 1,500 species collected. Although intensive field work continues to reveal novelties almost weekly, by now, most additions to the flora represent rare individuals or isolated populations. Concentrated collecting efforts, especially in areas and times of year previously missed, could turn up as many as a hundred new records over the next year. This is an underestimate if we begin to explore the recently acquired Vargas property. Col-

TABLE 1. The ten most diverse families and genera of flowering plants known from La Selva field station, based on collections through September 1980.

Family	Number of Species	Genus	Number of Species
Araceae	97	*Piper* (Piperaceae)	46
Rubiaceae	85	*Psychotria* (Rubiaceae)	32
Orchidaceae	68	*Philodendron* (Araceae)	31
Piperaceae	66	*Anthurium* (Araceae)	27
Melastomataceae	56	*Miconia* (Melastomataceae)	18
Leguminosae	55	*Peperomia* (Piperaceae)	17
Gramineae	53	*Ficus* (Moraceae)	16
Moraceae	37	*Calathea* (Marantaceae)	14
Euphorbiaceae	33	*Passiflora* (Passifloraceae)	13
Compositae	32	*Monstera* (Araceae)	13

lecting is planned to continue through 1982. The current rate of discovery and identification illustrates the folly of publishing lists or keys to the plants of La Selva at this time. Nevertheless, enough information has accumulated for us to give an accounting of the ten most diverse families and genera (Table 1). Other genera with ten or more species at La Selva include *Clidemia* (Melastomataceae), *Clusia* (Guttiferae), *Drymonia* (Gesneriaceae), *Heliconia* (Heliconiaceae), *Inga* (Leguminosae), *Panicum* (Gramineae), *Pleurothallis* (Orchidaceae), and *Solanum* (Solanaceae).

By comparison, the somewhat drier and more seasonal moist forest of Barro Colorado Island (BCI), Panama, roughly twice the size of La Selva, contains approximately 1,369 taxa (including subspecies) of vascular plants (Croat, 1978). BCI has more species in certain groups (Table 2), such as Leguminosae, which tend to be more xerophilic. La Selva is comparatively richer in mesophilic elements such as epiphytes (e.g., Araceae) and vascular cryptogams. Of the latter, La Selva has about 165 species as compared with 104 on BCI. Only two genera (*Cyperus* and *Epidendrum*) with ten or more species at BCI are not also represented by ten or more species at La Selva. The La Selva flora, however, contains at least nine such genera not so diverse at BCI.

The forest of Río Palenque, Ecuador, however, which like La Selva is wet forest, contains 1,033 species of vascular plants (Dodson & Gentry, 1978). The Río Palenque site encompasses an area of just 1.7 km^2 with only 0.8 km^2 in natural forest. All but one genus (*Epidendrum*) of the eight genera at Río Palenque with ten or more species are also represented by ten or more species at La Selva.

Because of intensive collecting, the La Selva Flora project is producing a series of collections of numerous undescribed species and many rare or inaccessible species whose fruits or flowers had been poorly known elsewhere. These are essential to our own identification process but also should prove of great interest to biogeographers, systematists and ecologists at large. Discoveries of new species are of course exciting and interesting on their own; the description of taxa new to science discovered at La Selva as a result of the flora project is only beginning (e.g., Grayum & Hammel, 1982). Often, however, the identification of already described taxa yields much more information. For example, a number of our oddities (rare or unusual taxa that had until recently defied iden-

TABLE 2. The ten most diverse families and genera of flowering plants from Barro Colorado Island, Panama, based on Croat, 1978.

Family	Number of Species	Genus	Number of Species
Leguminosae	110	*Piper* (Piperaceae)	21
Orchidaceae	90	*Psychotria* (Rubiaceae)	20
Gramineae	77	*Inga* (Leguminosae)	18
Rubiaceae	67	*Ficus* (Moraceae)	17
Araceae	44	*Miconia* (Melastomataceae)	14
Compositae	42	*Philodendron* (Araceae)	13
Melastomataceae	35	*Epidendrum* (Orchidaceae)	13
Moraceae	34	*Anthurium* (Araceae)	12
Piperaceae	31	*Cyperus* (Cyperaceae)	11
Bignoniaceae	29	*Solanum* (Solanaceae)	11

tification) emphasize the affinities of wet lowland Costa Rica with northern South America (Table 3), and apparently represent new records for Costa Rica and Central America.

FUTURE WORK

Among the families listed in Table 1, the most likely to increase in numbers of species known with further collecting are Gramineae, Leguminosae, Moraceae, Rubiaceae, and especially Orchidaceae, which may ultimately come to surpass even the Araceae. We expect that most future additions to the list will come from these five families, along with rarities from among other families, particularly those containing large trees, shrubby epiphytes, lianas, or inconspicuous understory herbs. Groups that are at once hard to collect and diverse such as Araceae, Bromeliaceae, Orchidaceae, *Clusia,* and *Ficus* are the most problematic. Families with a predominantly vine or liana habit are exceedingly abundant and have presented particular challenges at La Selva. Most such families are poorly known throughout the tropics.

If there is one point that has been driven home repeatedly during the course of collecting for this project, it is the astounding gap that still remains between the prevailing knowledge of what the neotropical flora contains and what is actually present. Finca La Selva has for 25 years been one of the most intensively studied parcels of land on the Caribbean slope of Central America. Consider, then, that the checklist of La Selva plants available at the beginning of this project included only 19 species of Araceae, and just three species of *Philodendron.* Recently, an authority on Araceae was able to more than double this total during the course of a one-hour visit (T. B. Croat, personal communication). It is our opinion that the tree flora, although fairly well known, still harbors many new records. Certainly the greater part of the silva is known due to the collecting efforts of foresters. At La Selva most of the tree species were accounted for early on by Leslie Holdridge and Gary Hartshorn.

We are constantly reminded that specialists in particular groups and botanists spending relatively long periods in the field are those most likely to find novelties and discern differences. Before the initiation of this project, for example, just ten

TABLE 3. Known distributions of some recently identified plants from La Selva.

Species	Reported Previously from
Amphidasya ambigua Standl. (Rubiaceae)	Panama & Colombia (Dwyer, 1980)
Asplundia antioquiae Harling (Cyclanthaceae)	Colombia (Harling, 1958)
Dicranostyles ampla Ducke (Convolvulaceae)	Brazil, Guyana, Venezuela (Austin, 1973)
Ferdinandusa panamensis Standl. & L. O. Wms. (Rubiaceae)	Panama, genus otherwise S. Amer. (Dwyer, 1980)
Moutabea sp. (Polygalaceae)	Panama, genus otherwise S. Amer. (Lewis & Herrera-MacBryde, 1969)
Psychotria microbotrys Ruiz & Standl. (Rubiaceae)	Bolivia to Venezuela (Standley, 1936)
Psychotria mima Standl.	Panama, Colombia, Brazil (Dwyer, 1980)

species of *Calathea* (Marantaceae) were known to occur at La Selva, but until recently none of us had concentrated on that group. One week of careful search for and examination of *Calathea* resulted in the addition of four more species to the list.

SOME SPECIFIC CONSIDERATIONS

It has become almost axiomatic among tropical systematic botanists that, in the course of a taxonomic revision, one starts with a large batch of names and reduces them by at least 50% (Madison, 1977; Rojo, 1972). Although this is the natural result (and a major purpose of revision) in most cases, our extensive field experience in Costa Rica and Panama suggests that important diversity in certain genera will be obscured if species are merged indiscriminately. Such merging is partly a result of a lack of decent specimens, but more a result of the inadequacy of using only herbarium specimens to distinguish species in some tropical genera (e.g., *Clusia* and *Philodendron*). Taxonomic conservatism is also supported by a natural and justifiable reluctance to recognize species based on one or a few poor sheets. We all wish to avoid the creation of "artificial endemism" that results from provincial taxonomy (D'Arcy, 1977).

Descriptions of new species from the tropics, not in conjunction with revisionary or monographic work, have undoubtedly resulted in many redundant names. However in certain genera there are probably many more species that have gone undetected for lack of field studies than there are superfluous names that have been applied for lack of careful literature search. *Philodendron*, *Clusia*, and *Asplundia* (Cyclanthaceae) are diverse genera of often bulky and inaccessible plants that in any case make very poor herbarium specimens. In these groups there may actually be more species than names in southern Central America. We cannot overemphasize the necessity for intensive field studies to accompany revisionary work in such genera.

CONCLUSION

Although Costa Rica is one of the more well-collected tropical countries (Prance, 1978), the figures are actually rather deceptive. Much of the wet Carib-

bean slope even today is quite inaccessible. Human population density is higher on the seasonally dry Pacific side where clearing of land for crops and cattle farming has left almost no lowland forests. The lack of a distinct dry season in the Caribbean lowlands, more than any other factor, has resulted in fewer people, fewer roads, and more forests. To that extent botanists are like other people; they too, for the most part, have avoided the hot humid Caribbean lowland forests in preference to the drier Pacific slope and cooler mountains. It is ironic that these poorly known remaining forests might be among the most diverse in Central America, because they, too, will soon be gone (cf. D'Arcy, 1977).

The Sarapiquí-Puerto Viejo area, which includes Finca La Selva, has been singled out as one of four very diverse and poorly known areas most in need of further collecting in Costa Rica (Gentry, 1978). La Selva, however, is not unique among Central American forests because of its diversity. It is probably representative of the wet Caribbean lowlands from adjacent Nicaragua through Panama into northern South America. This area is particularly rich in groups that in general have been avoided or ignored by collectors, a fact that only compounds the need for further collecting and field studies in the region.

The Caribbean forests are disappearing at an alarming rate. Day after day trucks overloaded with giant logs climb the winding gravel road to San Jose. While efforts to preserve large tracts of tropical forests are sometimes promising, sometimes depressing, we must continue to sample this definitely endangered habitat.

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NOTES

PSEUDOCROTON TINCTORIUS MUELL. ARG., A SYNONYM OF *CAPPARIS INDICA* (L.) FAWC. & RENDLE

In the herbarium of the Field Museum (F) in Chicago is a specimen (*Friedrichsthal 1072*) collected near Managua, Nicaragua, which is an isotype of *Pseudocroton tinctorius* Muell. Arg. (Flora 55:24. 1872), a monotypic genus referred by its author to the Euphorbiaceae. This species has intrigued me for some time, because it did not look like any euphorbiaceous genus known to me, had apparently not been collected since the type, and its relationships were obscure. In the protologue, Mueller placed it near *Leucocroton* Griseb., a West Indian genus that Webster (1975) referred to the tribe Adelieae, and Pax & Hoffman (1912:96) placed it in the Chrozophoreae near such genera as *Argythamnia* P. Brown, *Ditaxis* Vahl, and *Caperonia* St.-Hil. Webster (1975) left it out of his system of the Euphorbiaceae altogether because of the poor condition of the type and the consequent difficulty in placing it satisfactorily (Webster, pers. comm.).

Recently, while looking at the Central American species of *Capparis* L., I noticed that several of the lepidote species bore a striking resemblance to *Pseudocroton tinctorius*. Further examination revealed that the isotype of that species is exactly like *Capparis indica* (L.) Fawc. & Rendle, at least in its vegetative features such as lepidote indument, short petiole, and faint but readily apparent lateral veins and rounded apex of the leaf. The specimen of *Pseudocroton* at the Field Museum unfortunately lacks flowers. Mueller's description of the flower, however, accords exactly with very young flowers of *Capparis*, the important features being a 4-parted calyx, imbricate spatulate petals that are stellately pubescent, a disc of separate, extrastaminal glands that alternate with the petals, 16–20 short stamens, and a cylindrical-ovoid rudimentary ovary. Although the last two characters do describe the immature flowers of *Capparis*, they are in contrast to the mature flowers, which have strongly exserted stamens and long-stipitate ovaries. The immaturity of the flowers also accounts for Mueller's description of the plant as dioecious.

Thus, *Pseudocroton* falls into the synonymy of *Capparis*, and *P. tinctorius* becomes a synonym of *C. indica*, which is a widespread species of the West Indies, western and southern Mexico, Central America, and northern South America. I am indebted to Dr. Hugh H. Iltis of the University of Wisconsin, authority on the Capparidaceae, for confirming my identification of the type of *P. tinctorius* as *C. indica* and for assuring me that there are no potentially complicating taxonomic problems with *C. indica*, such as the existence of a Central American segregate species over which *P. tinctorius* might have priority.

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THE IDENTITY OF THE PANAMANIAN GENUS *DRESSLERIOPSIS* (RUBIACEAE)

In the treatment of the Rubiaceae for the Flora of Panama, Dwyer (1980) described the endemic and monospecific genus *Dressleriopsis* and erected, although invalidly, the new tribe Dressleriopsideae. The new genus, which is said to be unique among New World Rubiaceae in having 8-pyrened fruits, seemed to me to be similar to the paleotropical genus *Lasianthus* Jack. Subsequent study of some of the specimens cited by Dwyer (viz. *Mori & Kalunki 2340* and *Dwyer 9035*, both MO) confirmed that *Dressleriopsis* Dwyer is synonymous with *Lasianthus* Jack.

Lasianthus has its major centers of distribution in Asia (about 120 species) and Africa (about 20 species), but it has long been known that one species occurs in Cuba (Schumann, 1891:121).

Dressleriopsis panamensis shows all the characteristics of *Lasianthus* emphasized by Petit (1964:22; see also Denys, 1981): axillary inflorescences, fruits (Fig. 2) with many pyrenes opening by a basal lid, seeds with weak and oily endosperm, and large embryos. Because of the fruit and seed characters, Petit proposed transferring *Lasianthus* from the Psathureae to the Morindeae.

The following new combination is necessary:

Lasianthus panamensis (Dwyer) Robbrecht, comb. nov. *Dressleriopsis panamensis* Dwyer, Ann. Missouri Bot. Gard. 67:153. 1980. TYPE: Panama, *Dressler 3560* (MO, holotype, m.v.).

Lasianthus panamensis resembles the group of Asiatic species in which dense hairiness of the leaf-blade is found in conjunction with an asymmetrical base, such as in *L. attenuatus* Jack, *L. copelandii* Elm., *L. luzonensis* Elm., *L. rhinocerotis* Bl., and *L. wallichii* Wight, but within this group, *L. panamensis* is unique in being a low, mostly single-stemmed woody plant usually attaining a height of about half a meter and sometimes forming horizontal runners. This life-form, typical of the rain forest floor, is common in other groups of *Lasianthus* (e.g. the African *L. batangensis* K. Schum.), in the related genus *Trichostachys*

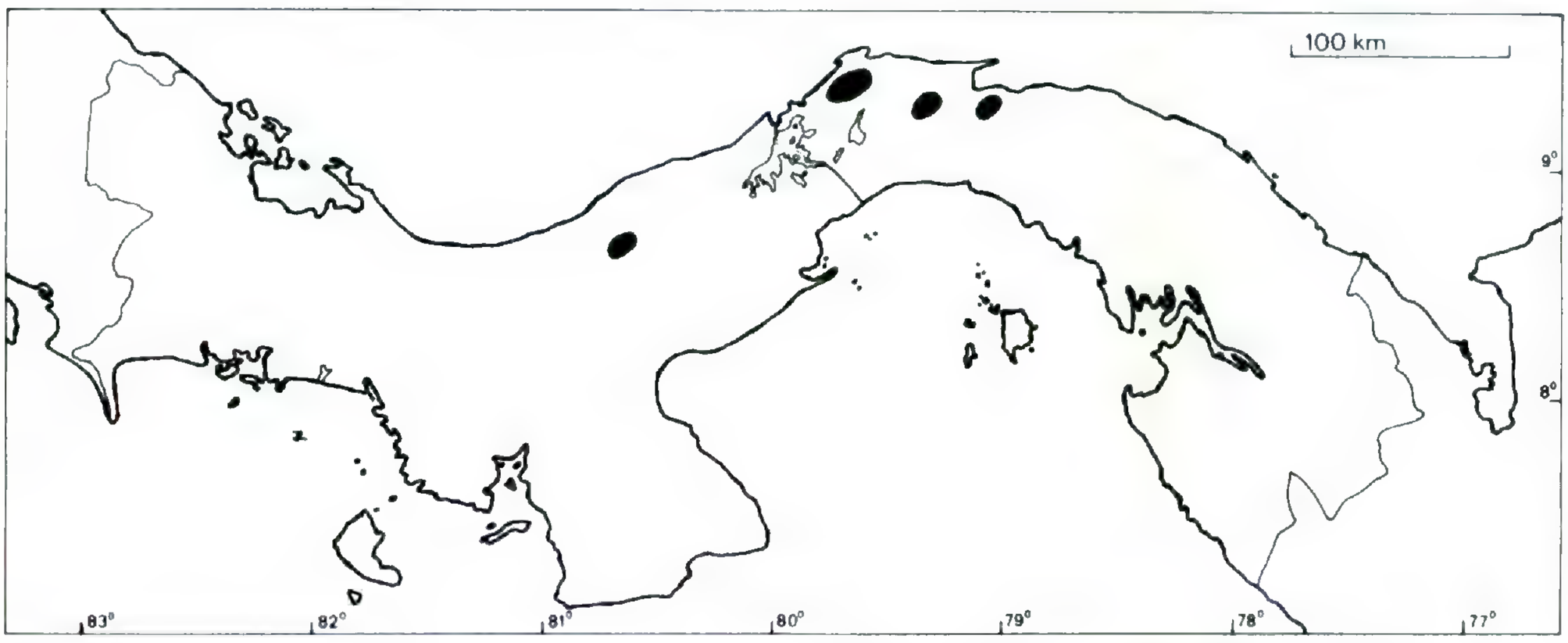

FIGURE 1. Known distribution of *Lasianthus panamensis* (Dwyer) Robbrecht.

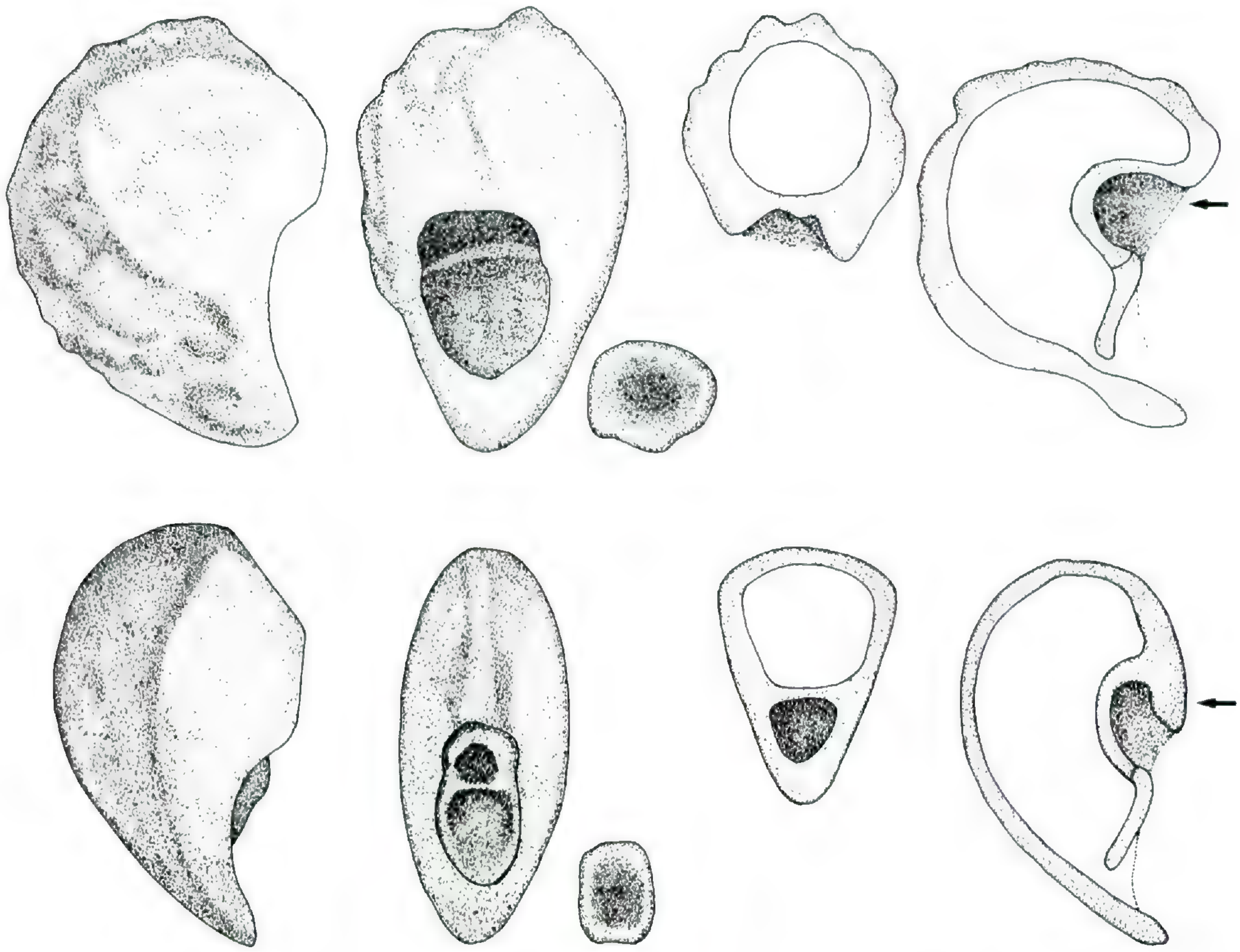

FIGURE 2. Pyrenes of *Lasianthus lanceolatus* (Griseb.) Wright ex Hook. (above; *C. Wright 253*, BR) and *Lasianthus panamensis* (Dwyer) Robbrecht (beneath; *Mori & Kallunki 2340*, MO). From left to right: lateral view, adaxial view (with basal lid removed), cross section (at level indicated in longitudinal section) and longitudinal section. All ×11.

and in many elements of the related tribe Psathureae. The formation of runners, which is very apparent in the recent collection from the province of Coclé (*Dressler 6017*), was described by Dwyer as the occurrence of "a pair of slender rigid opposite branches."

Lasianthus panamensis is certainly a distinct taxon, and there seems to be no doubt about its nativeness in Panama. It occurs in undisturbed forests and is frequent in at least three different areas with an extension of about 80 km from east to west in the part of Panama east of the Canal Zone (Dressler, personal communication). After the publication of *Dressleriopsis*, the taxon was also discovered about 100 km west of the Canal Zone: Panama, province of Coclé, W of Cano Sucio (trail to Chorro de Tife), ca. 13 km NNW of El Copé, very wet forest, 4 July 1981, *R. L. Dressler 6017* (BR). The species may extend as far west as Veraguas, or even into Bocas del Toro or Costa Rica (Fig. 1).

The other Neotropical *Lasianthus* does not occur on the Central American continent but is limited to the West Indies; its correct citation should be *L. lanceolatus* (Griseb.) Wright ex Hook. in Benth. & Hook., Gen. Pl. 2:129 (1873), and not *L. lanceolatus* (Griseb.) Urb. as is usually given (e.g. Alain, 1962). Hook-

er, although not formally, clearly proposes the transfer of *Hoffmannia lanceolata* to *Lasianthus* and refers to Wright for the idea. The differences between *L. panamensis* and *L. lanceolatus* are summarized in the following key:

Shrub up to 4 m tall without horizontal runners; leaf-blades 6–10 cm long and 2–3.5 cm wide, almost completely glabrous, with cuneate base symmetrical; pyrenes with a rough or grooved abaxial side. ---------- *L. lanceolatus*

Low, mostly single-stemmed, woody plants, sometimes forming horizontal runners; leaf-blades up to 23 cm long and 9 cm wide, with a very apparent hairiness, with rounded base often asymmetrical; pyrenes with a smooth abaxial side. ---------- *L. panamensis*

Pending a modern study of *Lasianthus*, the species discussed here can only be compared with Hooker's classification of the genus (1880) (taken over by Schumann, 1891:121). *Lasianthus lanceolatus* undoubtedly belongs to the series Nudiflorae. *Lasianthus panamensis* and the related Asiatic species mentioned above are harder to place and more or less agree with the series Bracteatae. In any event, the two Neotropical representatives of the genus *Lasianthus* are not closely related and seem to be the results of two separate cases of long distance dispersal.

I am grateful to the Director of MO for sending material on loan and to Dr. R. L. Dressler for valuable information and for sending his collection. Dr. J. H. Kirkbride, Jr., is gratefully acknowledged for his suggestions about the subject and for his review of the manuscript. I wish to thank Miss E. Denys for drawing the pyrenes and Mrs. M. Baudet-Allard for drawing the map.

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—Elmar Robbrecht, Nationale Plantentuin van België, Domein van Bouchout, B-1860 Meise, Belgium.

The previous issue of the Annals of the Missouri Botanical Garden, Vol. 69, No. 1, pp. 1–238, was published on 15 December 1982.

Musci Austro-Americani

G. Mitten

A reprint of the original, 1869, edition in The Journal of The Linnean Society, Botany, vol. XII, and the obituary by E. M. Holmes from the Proceedings of The Linnean Society, volume 119, 1907.

Although now well over 100 years old, Mitten's Musci Austro-Americani remains the only flora to attempt to treat all the mosses of the West Indies and Central and South America. Over 1,700 species are treated, of which about 600 were then new. Thus the work remains a fundamental reference for both the floristic and monographic muscologist.

With the cooperation of the Linnean Society, London, the Missouri Botanical Garden has reprinted this valuable work, which appeared in 1869 as Journal of the Linnean Society, Botany, volume 12, as a facsimile of the original, which is long out of print and very rarely available second-hand. The facsimile contains, in addition to the Musci, a reprint of E. M. Holmes' obituary of Mitten, which appeared in the Proceedings of the Linnean Society in 1907.

Musci Austro-Americani is a modern flora in format and content: there are keys, though they are usually not dichotomous; descriptions or diagnoses of each genus and species, always in Latin; and lists of specimens studied. An English introduction provides background information on Richard Spruce's collections, which formed the most important component of the collections available for Mitten's studies, as well as a discussion of the general characteristics of the neotropical moss flora.

Musci Austro-Americani is published as volume 7 of Monographs in Systematic Botany from the Missouri Botanical Garden. It is 672 pages long, including the appended obituary by Holmes, with sewn signatures and heavy paper covers.—MSB7.

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Illinois Convolvulaceae in the Missouri Botanical Garden Herbarium
Robert H. Mohlenbrock 393

Three New Species of *Aphelandra* (Acanthaceae) from Central America
Lucinda A. McDade 402

Xyris apureana Kral & Smith, A New Species of *Xyris* (Sect. *Nematopis*) from Venezuela *Robert Kral & Lyman B. Smith* 412

Xyris nigrescens Kral, a New Species of *Xyris* (Sect. *Nematopus*) from Costa Rica *Robert Kral* 415

Chromosome Number of *Byblis liniflora* Salisb. (Byblidaceae) *Ching-I Peng & Ann Kenton* 418

Preliminary Report on the Flora Project of La Selva Field Station, Costa Rica *Barry E. Hammel & Michael H. Grayum* 420

NOTES

Pseudocroton tinctorius Muell. Arg., a Synonym of *Capparis indica* (L.) Fawc. & Rendle *Michael Huft* 426

The Identity of the Panamanian Genus *Dressleriopsis* (Rubiaceae)
Elmar Robbrecht 427

The Ridgway Center, which is pictured on the cover of the ANNALS for the first time, was completed on July 18, 1982. It was designed to accommodate the Garden's many educational programs and to provide a place to orient visitors to the features of the Garden. The first floor contains the 400-seat Shoenberg Auditorium; plant and gift shop; entrance, ticket and information areas; orientation theater; educational classrooms and greenhouse; and a large floral display hall. The second level consists of educational and public relations offices; the Spink Gallery of porcelain art; and the Gardenview Restaurant. The building was designed by Hellmuth, Obata & Kassabaum, of St. Louis. It was funded by private donations in part and in part by a four-to-one match for a challenge grant from the National Endowment of the Arts.

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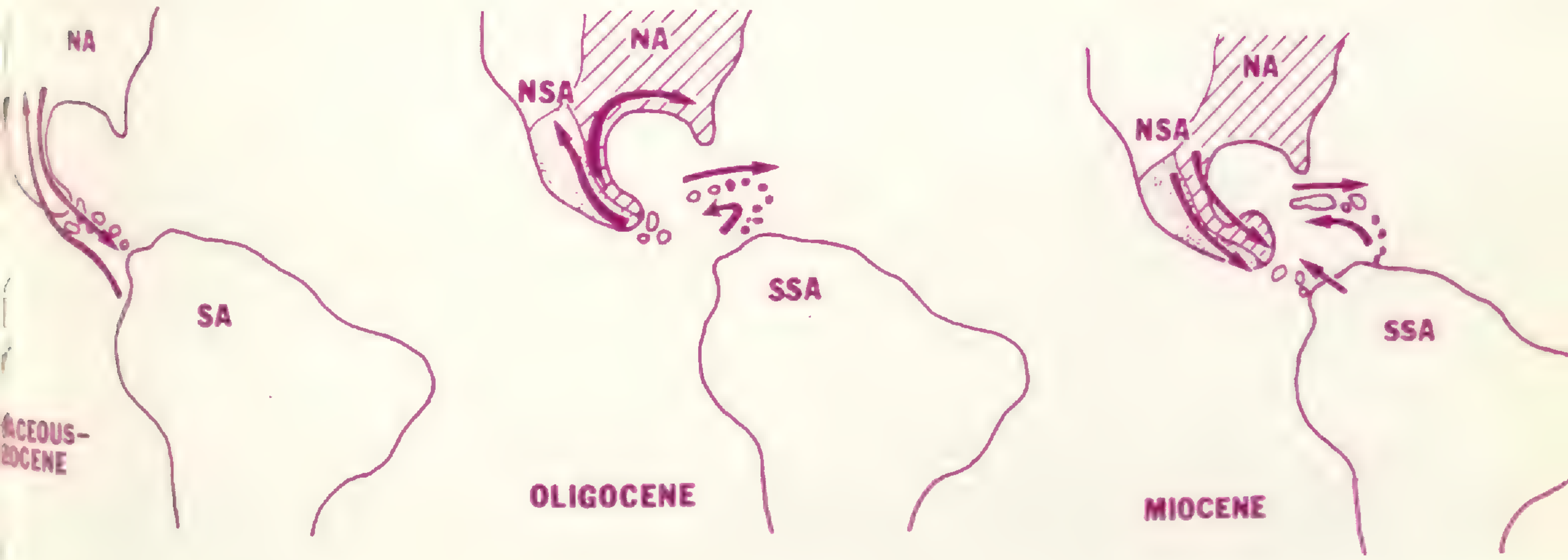
VOLUME 69 1982 NUMBER 3



CONTENTS

BIOLOGICAL STUDIES IN CENTRAL AMERICA: The Twenty-Eighth Annual Systematics Symposium *Nancy R. Morin* 431

Plate Tectonic Constraints on the Biogeography of Middle America and the Caribbean Region *Peter J. Coney* 432

Vicariance Biogeography in Mesoamerica *C. J. Humphries* 444

The Enigma of the Central American Herpetofauna: Dispersals or Vicariance? *Jay M Savage* 464

The Origin of the Pteridophyte Flora of Central America *Luis D. Gómez P.* 548

Neotropical Floristic Diversity: Phytogeographical Connections Between Central and South America, Pleistocene Climatic Fluctuations, or an Accident of the Andean Orogeny? *Alwyn H. Gentry* 557

PLANT GEOGRAPHICAL RESULTS OF CHANGING CENOZOIC BARRIERS

A Review of the Phytogeographic Evidences for Pleistocene Climate Changes in the Neotropics *Ghillean T. Prance* 594

Changing Cenozoic Barriers and the Australian Paleobotanical Record *Helene A. Martin* 625

Wallace's Line: A Result of Plate Tectonics *T. C. Whitmore* 668

Causes of Short-term Sequential Changes in Fossil Plant Assemblages: Some Considerations Based on a Miocene Flora of the Northwest United States *Aureal T. Cross & Ralph E. Taggart* 676

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BIOLOGICAL STUDIES IN CENTRAL AMERICA: The Twenty-eighth Annual Systematics Symposium

The Twenty-eighth Systematics Symposium at the Missouri Botanical Garden, held 16–17 October 1981, focused on the factors that have influenced the distribution of organisms in Central America. This topic is particularly timely in view of the recent initiation of a collaborative effort to write a flora of Mesoamerica, and in view of the current renewed interest in biogeographical processes.

The Missouri Botanical Garden has had a special interest in Central America since it began an intensive study of the flora of Panama in the early 1930s. Although the formal Flora of Panama was completed in 1981, much work is left to be done on the plants of this country alone. There is a need, however, for biological studies that go beyond the boundaries of individual countries and instead treat phenomena common to the biogeographical unit of Central America. For this reason the Missouri Botanical Garden, the Instituto de Biología de la Universidad Nacional Autónoma de México, and the British Museum (Natural History) have begun a collaborative effort to produce a synoptic flora in Spanish of the estimated 16,000 vascular plants of Mesoamerica, defined for purposes of the project as that area between the isthmus of Tehuantepec and the Panama-Colombia political boundary. This flora will serve as a concise identification manual of Mesoamerican plants.

In this symposium current information about geological events and distribution of organisms, both historical and contemporary, was presented to give an overview of the factors that have affected these distributions and the methods that are available for interpreting them. The symposium was supported in part by the National Science Foundation Grant DEB78-10180 to the Missouri Botanical Garden. Speakers at the symposium were Peter J. Coney, University of Arizona, Tucson; W. A. Clemens, University of California, Berkeley; Luis D. Gómez P., Museo Nacional, Costa Rica; Alwyn H. Gentry, Missouri Botanical Garden; Christopher J. Humphries, British Museum (Natural History); and Mario Sousa S., Universidad Nacional Autónoma de México. Clemens paper is not included here; the paper by Sousa was published by the three institutions collaborating on Flora Mesoamericana as the "Guide for Authors" and is available from any of the institutions on request.—Nancy R. Morin, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166.

Ann. Missouri Bot. Gard. 69: 431. 1982.

PLATE TECTONIC CONSTRAINTS ON THE BIOGEOGRAPHY OF MIDDLE AMERICA AND THE CARIBBEAN REGION

PETER J. CONEY[1]

ABSTRACT

North America-Eurasia and South America-Africa were certainly joined in the classic reconstruction of Pangaea by Middle Triassic time. The line of collision and suture included the Appalachian Quachita-Marathon orogenic trend in the United States extending southwestward into what is now northeastern and southeastern Mexico and into Guatemala. Widespread continentality prevailed and there was no Gulf of Mexico or Caribbean Sea. In Late Triassic time and continuing into Early Jurassic time this construct began to founder by initial rifting between South America-Africa and North America. No oceanic crust was formed, however, thus Africa-South America were still completely connected by land or shallow sea to North America until mid-Jurassic time. During this same uppermost Triassic to Middle Jurassic period a largely continental magmatic arc was draped across the Pacific margin of southwestern North America and apparently continued unbroken into northwestern South America.

Sometime in the Middle Jurassic oceanic crust began to form by seafloor spreading in the central Atlantic and Gulf of Mexico as separation of South America-Africa from North America accelerated. Once this dense crust began to form the trailing margins of the continents subsided below sea-level and construction of the Atlantic and Gulf coast continental shelves began. Evidence is quite conclusive that this ocean floor spreading did not reach the Pacific Ocean, but was transformed from the southwestern corner of the newly opened Gulf of Mexico northwestward across Mexico via a complex left-slip transform fault system that reached the Pacific margin near Los Angeles.

In Early Cretaceous time spreading continued in the central Atlantic but extended southward into the southern Atlantic. As the main axis of spreading extended into the south Atlantic, spreading ceased in the Gulf of Mexico. The south Atlantic spreading initiated separation of South America from Africa, but they probably remained in partial contact via ridge-ridge transform faults until Late Cretaceous time. South America must have finally completely separated from North America in Early Cretaceous time, probably via a rift along the eastern edge of Yucatan and the Nicaraguan rise.

By Late Jurassic time the Pacific continental margin arc had waned and was replaced by a complex, largely oceanic, magmatic arc whose position relative to southwestern North America and northwestern South America is not known. What we do know is that by Late Cretaceous-Early Tertiary time it had accreted against the Pacific margins of both. Connections between the continents are also not known but could have included a largely submarine magmatic arc, parts of which may have subsequently dispersed eastward as the Greater Antilles. Much of what is now Middle America is apparently underlain by oceanic crust at least as young as Late Cretaceous in age.

By Late Cretaceous time the Greater Antilles magmatic arc seems to have fully formed and subsequently moved northeastward as a northeast-facing subduction system during Late Cretaceous-Early Tertiary Laramide time.

The Greater Antilles arc-trench system ceased activity in Late Eocene time as it collided with Florida and the Bahama platform and as Laramide orogeny waned throughout western North America. This was followed by a major plate reorganization in the Caribbean-Middle America region nearly 40 m.y. B.P. which established the Caribbean plate more or less as we know it today. The principal change was initiation of the Lesser Antilles magmatic arc as an east-facing subduction system that began to consume Atlantic ocean floor. Also, a west-facing subduction system may have formed about this time along a proto-Central American western margin of the Caribbean plate. However, much of what is now Central America may have initially been off southern Mexico. The northern and southern margins of the Caribbean plate evolved into complex transform and transpressive systems as North and South America moved westward past a nearly stationary Caribbean plate. These motions significantly fragmented the Greater Antilles into their present array. There is no evidence for any complete land connection between North and South America via the Greater and/or Lesser Antilles throughout later Mesozoic or Tertiary time. Nor is there any evidence for complete land connection via Central America and the Isthmus of Panama before Neogene time.

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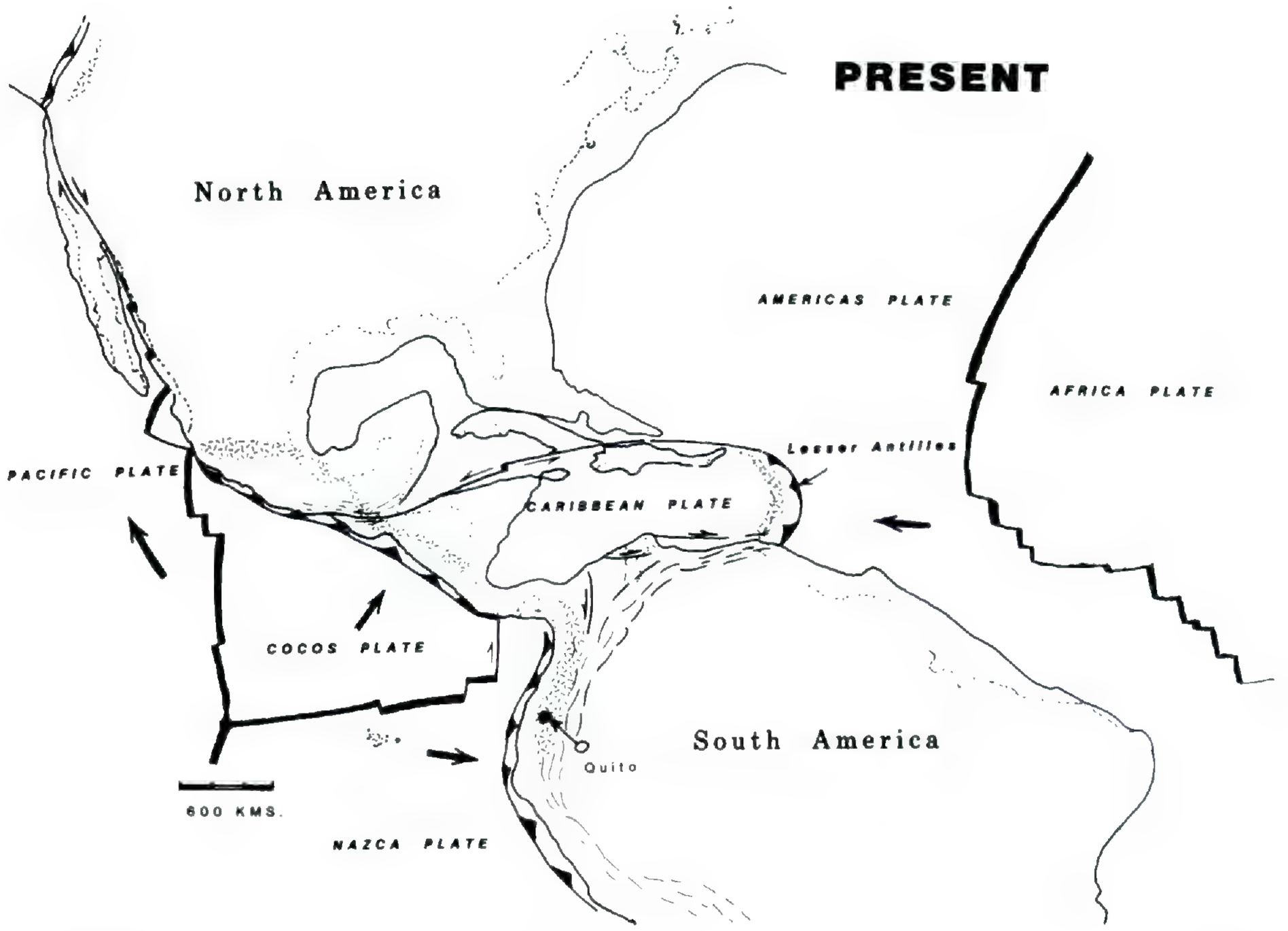

FIGURE 1. Present plate configuration. The six major plates and their motions are shown. Heavy black lines are spreading centers or rise crests; heavy, barbed lines are subduction zones; dashes pattern shows distribution of magmatic arcs. Dotted line is present coastline of the continents, solid line seaward is edge of continental crust. Opposed arrows on transform faults connecting rise crest segments show sense of relative motion on fault.

INTRODUCTION

Plate tectonics (see Cox, 1973) has provided for the first time a quantitative means to make reasonably accurate global paleogeographic reconstructions for Mesozoic-Cenozoic time. This new-found ability has enabled great insight into regional tectonic evolution of both the oceans and continents, and the implications for paleoclimatology, paleo-oceanography, and paleobiogeography are only just beginning to be fully explored. The objective of this paper is to outline plate tectonic arguments regarding the paleogeographic evolution of Middle America and the Caribbean region and adjacent North and South America (see also Dickinson & Coney, 1980). This hopefully can provide a paleotectonic background against which biogeographic arguments can be compared. It should be realized by the biogeographic community, however, that the resolution level of paleotectonic reconstruction is frequently coarser than that desired by biogeographers. In that sense it is possible that paleobiogeographic data may be as helpful to paleotectonics as is the reverse, which makes symposia such as this very propitious.

THE PROBLEM OF THE MIDDLE AMERICA-CARIBBEAN REGION

The present plate tectonic setting of the Middle America-Caribbean region is generalized in Fig. 1. The relationships are not simple and in their complexity

lies in part the problem of this region. Six plates are found here all interacting in a complex way.

The Pacific plate, which floors most of the Pacific Ocean, is moving[2] northwestward as it spreads away from the East Pacific rise. It is carrying Baja California and the State of California west of the San Andreas fault with it as it moves. The Cocos plate is moving northeastward away from the East Pacific rise and Galapagos rise and is being subducted beneath southern Mexico and Middle America along the Middle America trench. The Nazca plate moves eastward away from the East Pacific rise and Galapagos rise and is subducting beneath South America. North and South America, probably as separate plates, move generally westerly away from the Mid-Atlantic rise. Caught in the middle of all these motions is the Caribbean plate. Its motion is not well known, but it is probably moving very slowly if it is not essentially stationary. The Caribbean plate subducts Atlantic sea-floor beneath the Lesser Antilles on the east, and Cocos and Nazca plate beneath the Middle America region on the west. Its northern boundary is a complex transform fault system and its southern boundary is an even more complex transform-transpressive fault system. Both of these fault systems accommodate the motions of North and South America as they move generally westward past the Caribbean plate. They are probably slightly converging one upon the other and upon the Caribbean plate as they move.

The problem in the Caribbean region is that the two "Atlantic" plates of the Americas and the three "Pacific" plates all spread from rise crests and thus leave magnetic anomalies painted on the sea-floor as they spread. This allows, by backing-up dated anomalies sequentially to the rise crest, rather accurate reconstructions of relative plate positions. In contrast, no such data exists for the Caribbean plate, since, with the exception of a small rise crest in the Cayman trough, it is surrounded by subduction zones or transform faults. As a result, no complete record of motion with respect to other plates is preserved. Therefore the history of the Caribbean plate must be deduced from controlled motions of adjoining plates combined with the geologic and geophysical (see Martin & Case, 1975; and other papers in Nairu & Stehli, 1975) record preserved on the Caribbean plate itself. This kind of information is at best always somewhat equivocal and subject to varied interpretation. The model proposed here is perhaps one of several permissible interpretations (for example, see Malfait & Dinkelman, 1972). Certainly, in a region as poorly known and complex as this one, new information and insight

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[2] Plate motions can only be described as motions with respect to some frame of reference. There are two general methods. In purely relative motion schemes the motion of a plate is described with respect to an adjacent plate, which for computational purposes is assumed to be fixed (see Ladd, 1976). A second approach is the so-called "absolute" motion scheme. Here plate motions are described with respect to some reference frame outside the plates themselves. Usually the chosen frame is the assumed rotational axis of the earth which is derived from paleomagnetic data and from the positions of assumed semi-fixed thermal anomalies or "hot spots" in the mantle. These "hot spots" produce intra-plate volcanism such as the Hawaiian Islands. As a plate moves over a "hot spot" a trail of volcanic edifices such as the Hawaii-Emperor seamount chain can be produced. If the edifices can be dated an "absolute" motion of the plate is derived. Then, using relative motions between this plate and other plates, the motions of all the plates with respect to the fixed reference frame can be attained. The motions discussed in this report are this second, or "absolute," type (see Coney, 1978).

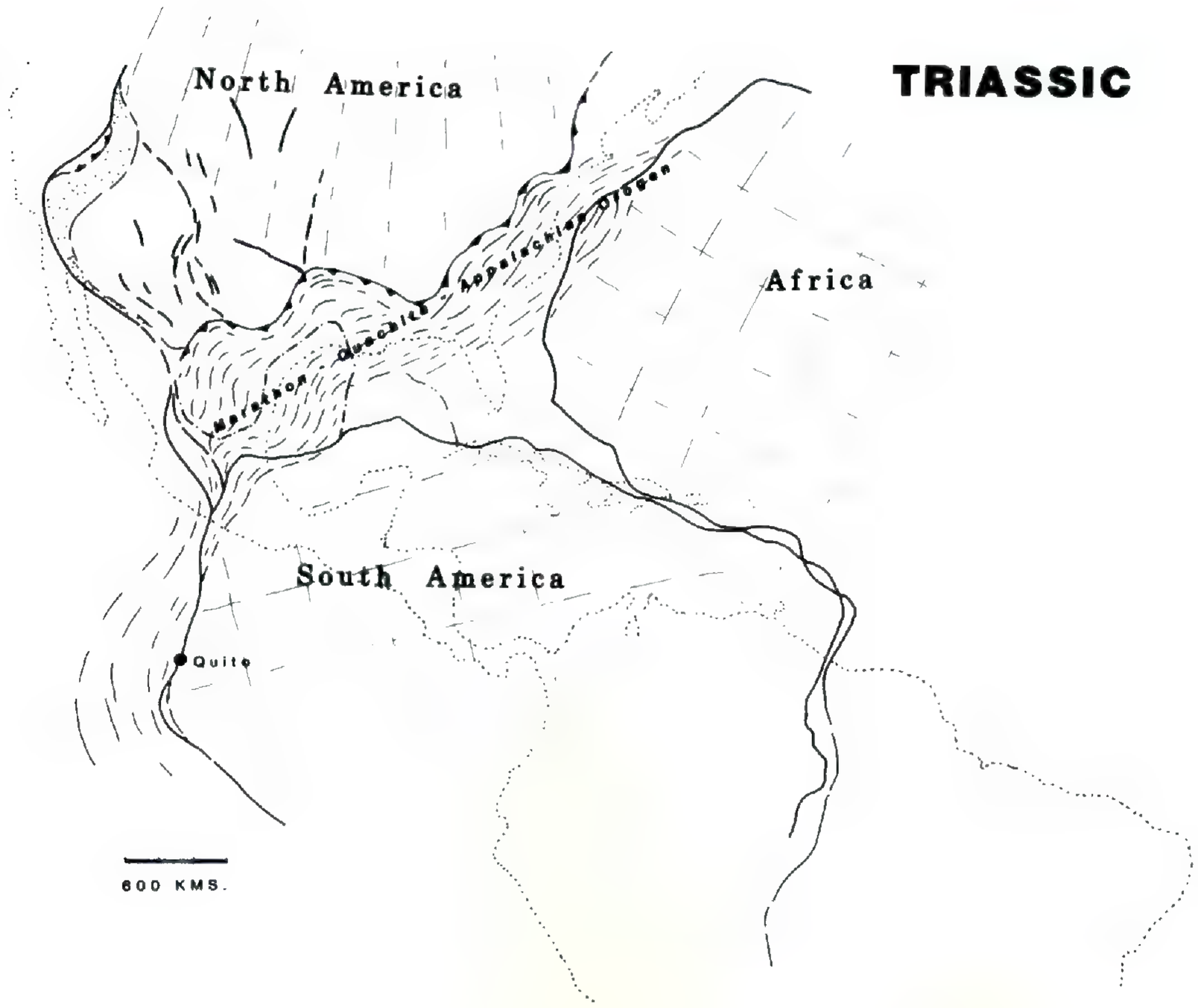

FIGURE 2. Triassic plate configuration. Dashed light lines forming grid are generalized present-day lines of latitude and longitude. Deformation associated with the Appalachian-Marathon-Quachita orogeny shown by wavy lines. Dot pattern is Cordilleran miogeocline.

could force significant revision of today's conceptions, including what is presented here.

TRIASSIC

The reconstruction for Triassic time is shown in Fig. 2. It is the classic configuration of Pangaea (see Irving, 1977) as manifested in the Caribbean-Middle America region. This reconstruction derives from closure of the central Atlantic Ocean controlled by the magnetic anomalies there, which places Africa close against the margin of eastern North America. Since South America was still stitched to Africa at this time, what one does with Africa one must also do with South America. This predetermines the position of South America with respect to North America. South America is shown overlapping all of what today is the Caribbean Sea, Middle America, and almost one-half of Mexico. This is a geometric fact from which one must conclude that all the rocks and lands included within the overlapped region either did not exist at this time or they were somewhere else (Coney, 1978).

The assumption is that the line of suture between Africa-South America and North America resulted from Late Paleozoic collision and possible right-lateral strike-slip faulting between the two continental masses to produce the Appalachian-Quachita mountain system (Graham et al., 1975). The final consolidation, certainly completed by Late Triassic time, is the reconstruction shown in Fig.

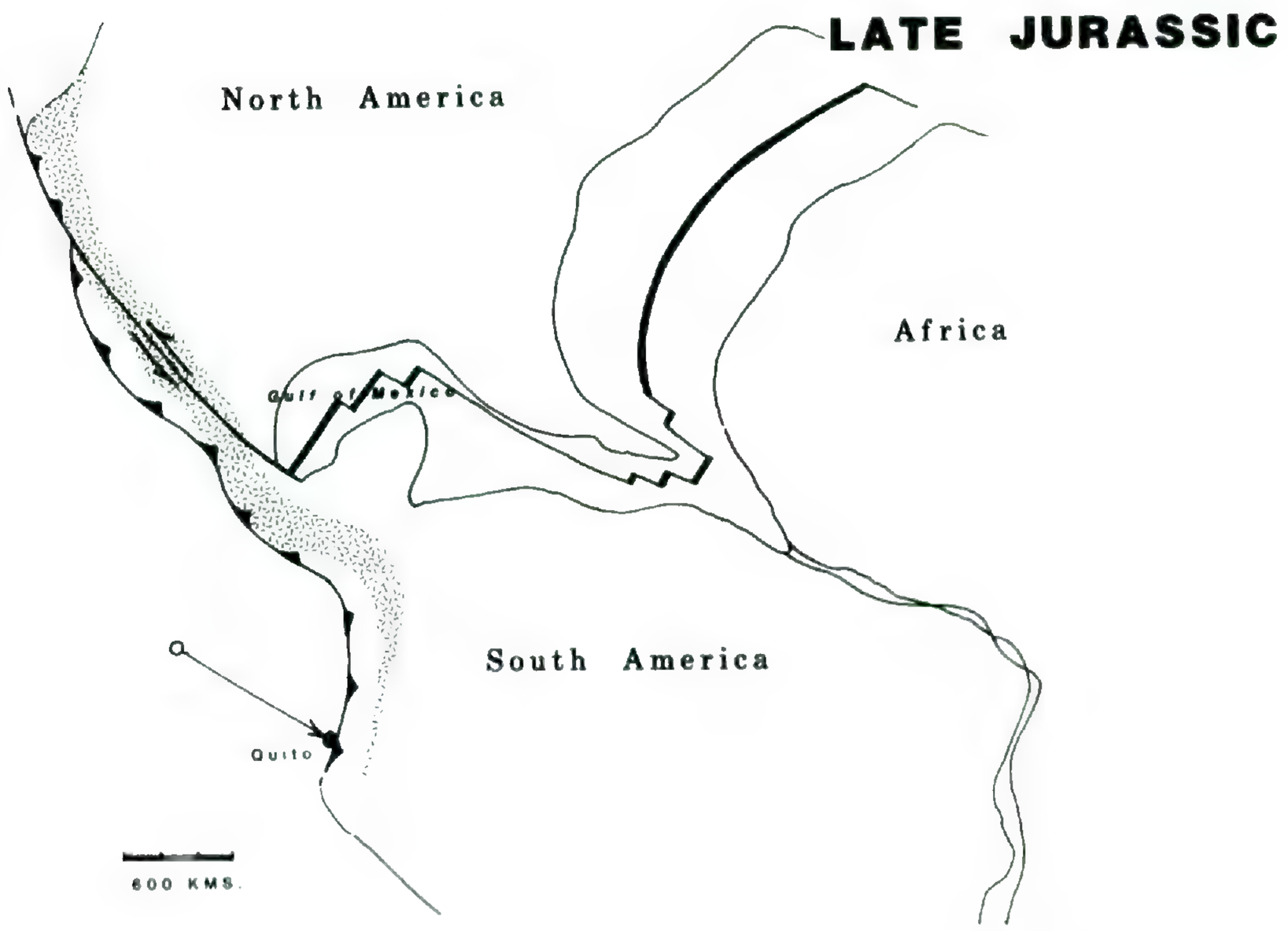

FIGURE 3. Late Jurassic plate configuration. On this and subsequent figures the position of Quito, Equador is shown with respect to North America assumed fixed. The arrow indicates the amount of movement this position made during the period following the previous figure. The Mojave-Sonora "megashear" is shown by heavy line with opposed arrows indicating sense of movement.

2. Widespread continentality prevailed throughout the region and there was no Gulf of Mexico or Caribbean Sea, nor any Atlantic Ocean. In short, Africa-South America-North America were a single landmass and the region was everywhere above sea-level.

LATE JURASSIC

The reconstruction for Late Jurassic (Fig. 3) shows the central Atlantic Ocean and Gulf of Mexico opened as Africa-South America separated from North America. Paleomagnetic data suggests that North America moved rapidly northwestward relative to a near-stationary Africa-South America. The process of rifting and separation probably began in Late Triassic time by inception of extension between the two major blocks. There is considerable geologic and geophysical evidence for widespread development of rift valleys and ridges as continental crust began to extend. Continentality prevailed as the rifted basins filled with debris shed off adjacent highlands and uplifted blocks. By Middle Jurassic time extension had reached sufficient amounts such that inter-connected down-faulted and subsided areas allowed distal incursions of shallow marine water, probably from the Tethys Ocean north of Africa and south of Europe. Evaporation of these incursions produced widespread salt and other evaporite deposits that are well known throughout the Gulf of Mexico region today.

Once oceanic crust began to form in Middle Jurassic time the margins of the newly rifted continental masses began to subside rapidly due to higher density of new oceanic material and thermal decay of the continental margins. This allowed

widespread marine transgression upon the newly formed continental margins from the Atlantic and Gulf of Mexico oceanic basins. The transgressions initiated development of the continental shelves as sediments were draped across the bared edges of the continents. This decelerating process of shelf development has continued to the present time.

There is some evidence to suggest that the young rift between Africa-South America and North America did not reach the Pacific Ocean. It appears to have been transformed northwesterly across Mexico as a major left-slip fault system. This complex fault may have extended from the southwestern corner of the newly opening Gulf of Mexico northwestward to the Pacific coast near Los Angeles in southern California. This important feature has been termed the Mojave-Sonora "megashear" and estimates are that up to 800 kilometers of left-slip movement took place along it between Late Triassic and Late Jurassic time (Silver & Anderson, 1974).

During this same period, between Late Triassic and Late Jurassic time, a volcanic-magmatic arc developed along the Pacific margin of North and South America. The feature seems to have been almost everywhere above sea level standing on continental crust and extending unbroken between the two continents. The implication is that in spite of over 800 kilometers of relative separation between Africa-South America and North America, and in spite of the formation of the central Atlantic Ocean and Gulf of Mexico as deep marine basins between them, the two supercontinents remained in above or near sea-level contact via Mexico until Late Jurassic-Early Cretaceous time. That Africa and South America were still joined, thus both in contact with North America via Mexico, has significant implications for Jurassic reptilian interchange between East Africa and western United States (Galton, 1977).

Early Cretaceous

The reconstruction for Early Cretaceous time is the least reliable and subject to considerable uncertainty. Based on the spreading history in the central Atlantic, we know that Africa continued to separate from North America, but spreading in the Gulf of Mexico apparently ended by Late Jurassic time. We also know that spreading between Africa and South America began in Early Cretaceous time. These geometric facts demand continued separation of South America from North America but without spreading and transform movements in the Gulf of Mexico and along the Mojave-Sonora megashear. This necessitates spreading between the two continents in what might be termed a proto-Caribbean sea (Fig. 4). It must be recalled, however, that no record of this spreading has been positively identified to date. It is simply a construct apparently demanded by plate geometry.

By Late Jurassic time the Pacific margin-continental margin magmatic arc had waned and was replaced by a complex, largely submarine oceanic magmatic arc whose position was apparently somewhere off-shore of the Jurassic continental margin (Campa & Coney, in press). The hypothetical spreading center between North and South America may have extended southwestward to join with various Pacific spreading centers. If correct, a deep ocean basin may have separated North America and South America during part of Early Cretaceous time.

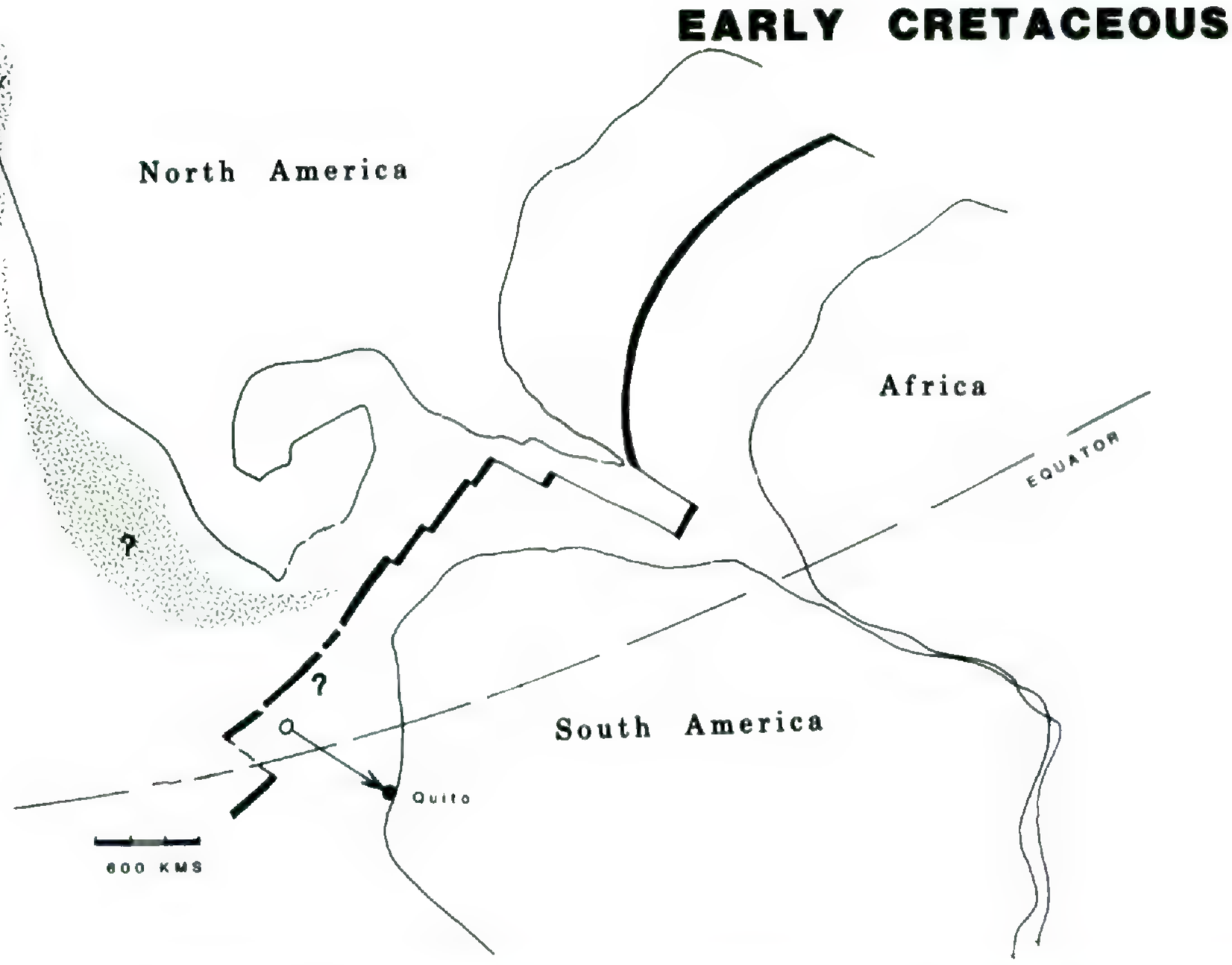

FIGURE 4. Early Cretaceous plate configuration. Symbols as on previous figures. The assumed spreading center between North and South America is shown projecting into the Pacific Ocean.

LATE CRETACEOUS

The reconstruction for Late Cretaceous (Fig. 5) is nearly as equivocal as that for Early Cretaceous and it is certainly plagued by uncertainties that may be years from resolution. Spreading had started in the south Atlantic separating Africa from South America, but these continents were perhaps in close contact across transform faults between northeastern Brazil and the west African coast. The principal enigma, however, is the geology between North and South America.

We do know that on several islands of the Greater Antilles rocks at least as old as Middle Cretaceous have the aspect of a submarine volcanic arc (see Khudoley & Meyerhoff, 1971). This suggests the proto-Greater Antilles formed as a submarine volcanic chain that presumably stood above a subduction zone. The most likely location of this subduction zone was off-shore of the Pacific-American margin far to the southwest of the present position of the Greater Antilles. It may have been part of the off-shore Cretaceous arc discussed earlier that stood southwest of Mexico. This arc apparently had accreted against North America by Late Cretaceous-Early Tertiary time and may have simply extended southeastward across the growing gap between North and South America. It was subsequently swept northeastward through the widening gap that was to become the Caribbean Sea.

The Cretaceous arc is of interest, if it existed as portrayed, since it could have harbored faunas and floras upon its far-flung volcanic islands, which were swept eastward as the arc migrated toward its present position. It could have also provided "stepping stones" for dispersals between the two continents during

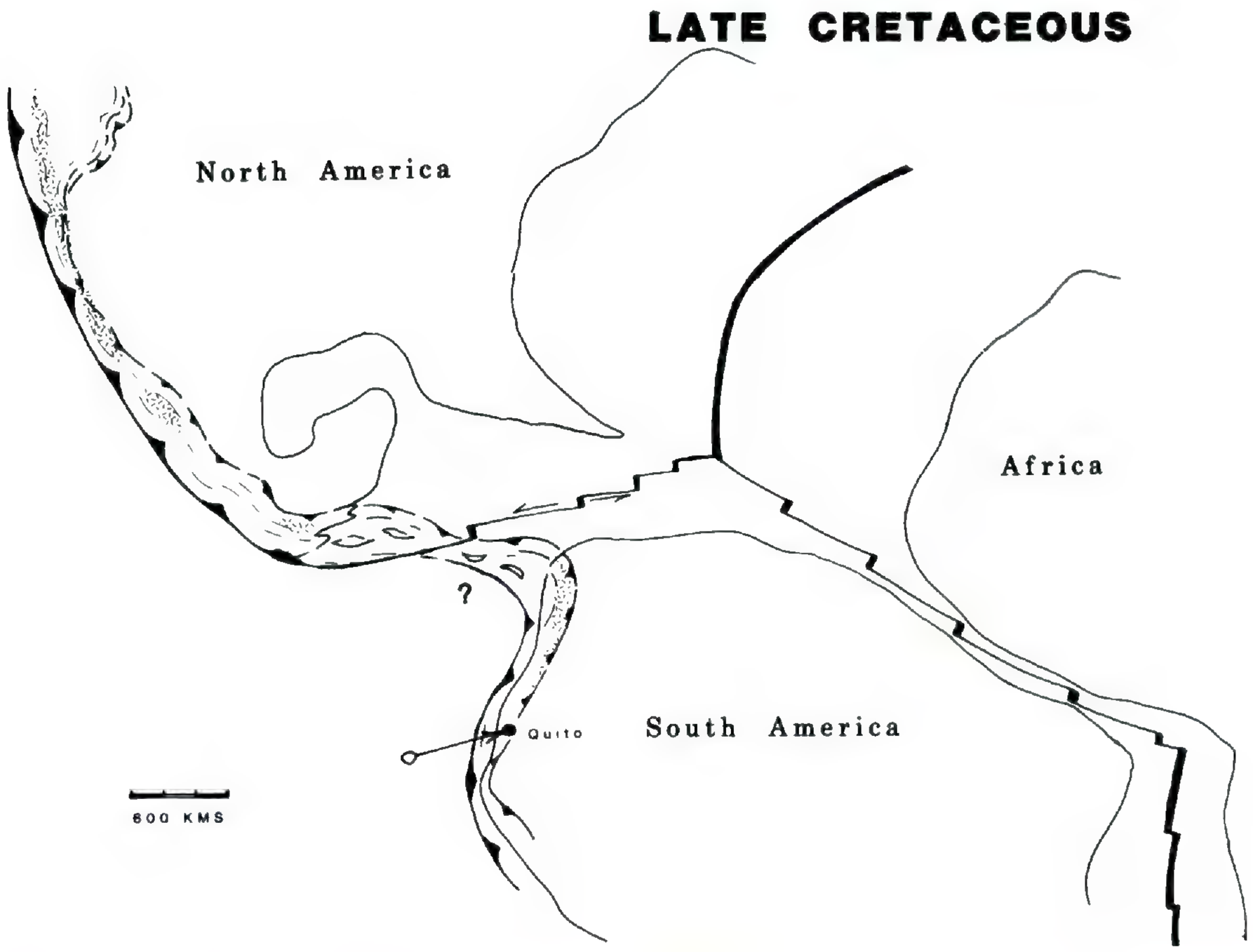

FIGURE 5. Late Cretaceous plate configuration. Symbols as on previous figures. The Cretaceous volcanic arc is shown accreting against North and South America and connecting the two continents by scattered volcanic islands.

Middle and Late Cretaceous time. The linkage was, however, no more than scattered islands and fringing reefs, probably much like present-day Lesser Antilles.

EOCENE

The Eocene reconstruction (Fig. 6) represents events that culminated from Late Cretaceous to Early Tertiary Laramide orogeny as manifested in the Middle America-Caribbean region. This important orogeny affected the entire North American Cordillera and was important in the Andes of South America as well. It seems to have resulted in part from accelerated convergence rates between one or more oceanic plates in the Pacific realm and the North and South America plates. It may have also been influenced by large scale accretions to the Cordilleran margin of "suspect" (Coney et al., 1980) submarine arcs and lesser lithospheric scraps during this time.

The principal result of Laramide orogeny in the Middle America-Caribbean region was the development of the Greater Antilles as a northeast facing subduction system composed of a largely submarine magmatic arc with a trench on its northeast side (Dickinson & Coney, 1980). The interpretation presented here is that the arc-trench system migrated northeastward relative to North America subducting proto-Caribbean sea-floor beneath it as it moved. This motion eventually caused the system to collide with the Florida-Bahama platform in Eocene

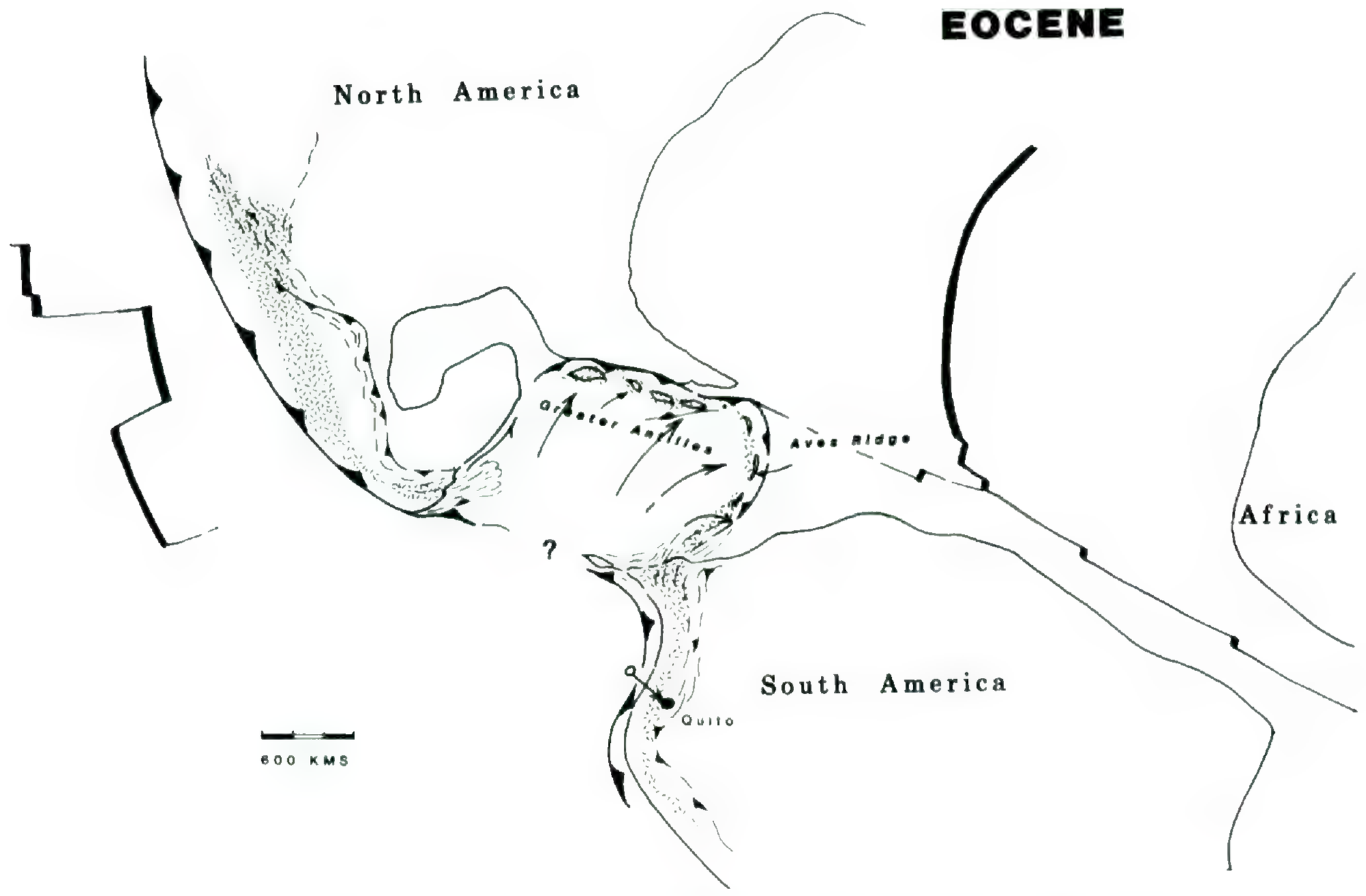

FIGURE 6. Eocene plate configuration. Symbols as on previous figures. The Greater Antilles is shown sweeping into the gap between North and South America and colliding with Florida and the Bahama platform. Soon after the time of this figure plate geometry changed to produce the features shown on Fig. 1.

time. It is assumed that the western end of the system slid northward along a transform fault past the eastern edge of the Yucatan Peninsula. The eastern end of the system is somewhat conjectural, but may have included the now submarine Aves ridge and perhaps part of the Venezuelan Coast Ranges. Paleomagnetic data from several parts of the Greater Antilles-Venezuelan Coast Ranges system suggest significant translations and rotations (see MacDonald & Opdyke, 1972).

If the model presented above is correct, it is assumed that parts of the Greater Antilles may have evolved from the arc system shown on Figs. 3 and 4 for Early and Late Cretaceous time. This arc would then have subsequently swept northeastward and fragmented into the widening gap between North and South America. At all times the system was apparently largely composed of submarine volcanic edifices that occasionally rose above sea-level to form scattered volcanic islands and fringing reefs. These constructions may have partially coalesced by Eocene time. The contact with South America via the eastern end of the system was probably less complete than the contact at the western end with North America. This was because the arc-trench system was forced to extend itself southeastward with time as the two continents continued to separate, and since the arc was actually moving obliquely away from South America.

MIDDLE AND LATE TERTIARY

The Greater Antilles arc-trench system ceased activity in Late Eocene time as it collided with Florida and the Bahama platform. This waning of arc activity

was coincident in time with the waning of Laramide orogeny throughout western North America. What followed was a major plate reorganization in the Middle America-Caribbean region, which established the Caribbean plate more or less as we know it today (Fig. 1).

The Caribbean plate was formed by initiation of the Lesser Antilles magmatic arc as an east-facing subduction system that began to consume Atlantic Ocean sea-floor. There is no evidence of the existence of the Lesser Antilles prior to Late Eocene-Early Oligocene time. The arc-trench system seems to have formed just east of the by then extinct Aves ridge. The western edge of the Caribbean plate apparently was a southwest facing arc-trench system along what today is the west side of Middle America. The northern and southern margins of the Caribbean plate evolved into complex transform and transpressive systems as North and South America moved westward and northwestward respectively past a nearly stationary Caribbean plate.

If this model is correct, the Caribbean plate must have been almost 700 kilometers west of its present position with respect to North America and South America. This means proto-Middle America lay south of southern Mexico and the Lesser Antilles southeast of the Bahama platform. The motions of North and South America swept the Caribbean plate relatively eastward and fragmented the Greater Antilles into their present array with Cuba transferred to the North America plate as the Cayman transform evolved. The southern margin of the Caribbean plate was more transpressive since South America's motion was more obliquely northwestward. This has sheared and compressed the Venezuelan Coast Ranges and thrust them southeastward onto South America. The northwesterly motion of South America also served to shorten the distance between North and South America, causing South America to compress and overthrust the Caribbean plate at its western end. This may have flexed the Middle America region into the present twist now seen in Panama and along with collision served to aid in raising it above sea-level in Late Tertiary time to produce the all important land-bridge between the continents (see Case, 1974).

In contrast to the Laramide Greater Antilles, the Cenozoic Lesser Antilles seem to have been much more closely tied at their southern end to South America as they migrated eastward along the Venezuelan coast. Also, the growth and development of a sub-aerial Middle America south of the transform fault zone in Guatemala seems to have progressed southward and eastward toward South America with the final link being collision between Panama and South America in Pliocene time.

Some Summary and Broad Biogeographic Implications

1. During Triassic and Early Jurassic time, widespread continentality prevailed across the entire region and North America-South America-Africa were one landmass part of the super-continent of Pangaea.

2. By Middle Jurassic time, the central Atlantic and Gulf of Mexico opened and by Late Jurassic time both were floored by deep marine oceanic crust. A land connection between Africa-South America and North America persisted via Mexico, however, until Late Jurassic time.

3. During a brief period in Early Cretaceous time, North and South America may have been separated by a spreading center and a growing deep marine basin. Spreading started between Africa and South America in Early Cretaceous time, but land contact may have persisted locally via transform fault margins off present-day northeastern Brazil until Late Cretaceous time.

4. Perhaps as early as Aptian-Albian time a submarine volcanic arc may have provided a connection via scattered volcanic islands between southern Mexico and Colombia-Venezuela. Parts of this arc may have subsequently swept northeastward as the Greater Antilles.

5. The Greater Antilles were perhaps most closely tied to North America via Yucatan and eventually through collision with Florida.

6. The Lesser Antilles were (as they are today) more closely tied to South America during their development from Late Eocene to the present time.

7. Middle America grew sub-aerially southward from North America as a complex volcanic arc-trench system, eventually forming the final land bridge by collision south of Panama in Pliocene time.

8. If overland dispersals between North and South America occurred, they would have been most favored during Triassic and Early Jurassic continentality, then again in Late Tertiary time via the land bridge in Panama. They could have persisted into Late Jurassic time via Mexico. From Late Jurassic to Late Tertiary time only inter-island passages were available.

9. Permo-Triassic non-marine life-forms could have been stranded by isolation on North America and South America from fragmentation of Pangaea. Any landlocked life-forms in the Greater Antilles should be less than Late Jurassic-earliest Cretaceous in age and survival would depend on ability to cope with widely separated and shifting island habitats. Jamaica and Middle America seem more closely tied to Mexico than the Greater Antilles. Finally, there has been considerable fragmentation of the ancestral Greater Antilles through post-Eocene strike-slip faulting between the North American and Caribbean plates.

EPILOGUE

The biogeographic community should be aware that recent developments in the geological sciences strongly suggest that even within the mobilistic concept of plate tectonics there has apparently been considerably more mobility in the evolution of continental margin mountain systems, such as the American Cordilleras, than was recognized only several years ago. The record in western North America, for example (Coney et al., 1980; Coney, 1981), shows that all of Alaska, two-thirds of the Cordillera in western Canada, about 50% of the Cordillera in western United States, and as much as 80% of Mexico (Campa & Coney, in press) are made up of what are termed "suspect terranes." These terranes are suspect because paleogeographic continuity with the cratonic old part of North America cannot be proven through large periods of post-Precambrian time. Paleomagnetic data, stratigraphic and structural data, and distributions of faunas

support the concept that many of the terranes are fragments of various sorts swept against North America, some from far-flung reaches of the Pacific Ocean. Most of the accretions onto North America occurred since Middle Jurassic time. The biogeographic implications of all this have hardly begun to be explored.

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VICARIANCE BIOGEOGRAPHY IN MESOAMERICA

C. J. HUMPHRIES[1]

ABSTRACT

This paper sets out to achieve three objectives. A brief introduction gives the present position of cladistic biogeography. Secondly, the most recent developments in cladistic biogeography for resolving complex and apparently incongruent species cladograms are presented. Thirdly, the methods as applied to the interrelationships of endemic areas in Mesoamerica with particular respect to the data of Rosen (1975, 1978, 1979) on poeciliid fishes is given.

INTRODUCTION

The analysis of spatial and temporal distribution of life on earth is the principal concern of historical biogeographers. Although many people would agree with this statement, there is still considerable disagreement amongst biogeographers about which methods should be used for the study of distribution and how distributions contribute information about the interrelationships and origins of areas. Distribution patterns can be analyzed in at least three different ways: first, we can compare the number of species or groups of species in different regions and say how many are common to each, thus getting a measure of overall similarity. Second, we can note the species and genera within one region and compare them with the species and genera of another and speculate where and how they might have arrived there. Third, we can make a comparison of the cladistic relations of various groups of organisms occurring in a group of areas of endemism to develop hypotheses on the historical connections of biotas in space and time—the pursuit originally identified by Nelson (1975) and Nelson and Rosen (1981) as vicariance biogeography and called cladistic biogeography by Parenti (1981).

Historical biogeography, by any method, is an integration of taxonomy and historical earth science. A comparison of taxonomies in different groups is the basis for determining biogeographic patterns. Historical biogeography is thus an integral part of systematics and a slave to its theoretical foundations. Invariably, changes in historical biogeographic theory follow changes in taxonomic theory. There have been numerous developments in the post-war period and today major divisions exist between the practitioners of cladistics, evolutionary systematics, and phenetics with parallel divisions in historical biogeography between the methods of cladistic biogeography (e.g., Nelson & Platnick, 1981), dispersalism (Darlington, 1965), and area phenetics (e.g., Holloway & Jardine 1968). I would like to concentrate my efforts on the most recent and most thorough developments in systematics and biogeography—cladistics and vicariance. Most of the ideas presented here do not claim my originality, but are the ideas of three zoologists from the American Museum of Natural History—D. E. Rosen, G. Nelson, and N. I. Platnick—and one botanist, L. Croizat, now resident in Vene-

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zuela, who have all done so much to put historical biogeography into a scientific framework.

In the view of Patterson (1981), analytical systematics has been developed by three groups of workers: those workers who have adopted numerical methods for explicit phylogeny construction (e.g., Kluge & Farris, 1969; Farris et al., 1970; Farris, 1970); those taxonomists like myself influenced originally by Hennig's phylogenetic systematics (see Hennig, 1965, 1966); and those biochemists who have independently developed methods of reconstructing phylogenies from molecular data (e.g., Fitch & Margoliash, 1967; Moore et al., 1973; Fitch, 1977). These methods all have various features in common which distinguish them from narrative procedures. They all have taxa or empirical units as terminal branches in the relationship diagrams and the method for producing the diagrams is to interpret the most economical or most parsimonious distribution of homologies (i.e., characters, components, synapomorphies) (Patterson, 1981). As the basic method for producing the diagrams was developed independently in the three different fields, its superiority over narrative methods lies in its simplicity and its accessibility to criticism. By insisting on one property—homology, and only one criterion—parsimony, cladistics is as scientific a method as anyone can use in systematics. Narrative systematics on the other hand allows any explanation and thus immunizes itself against criticism.

Patterson (1981) when reviewing the recent history of efforts to clarify the basis of historical biogeography concludes that cladistic biogeography is a development within cladistics. Analytical or vicariance biogeography is the pursuit of a method which encompasses a code comparable to cladistics. By gradually shedding *a priori* assumptions such as dispersal, extinction, allopatry, and sympatry it has increased our chances of understanding pattern and area interrelationships without circular evolutionary reasoning. In other words, if we are to understand the products of evolution we cannot use the existing principles to interpret patterns. By changing the word homologies to sister groups cladistic biogeography interprets the geographical distribution of sister groups parsimoniously. Different patterns when added together generate general hypotheses of area interrelationships. Thus, by using the two criteria of monophyletic sister groups and parsimony, cladistic biogeography is as scientific a method as anyone can use in historical biogeography.

Biogeographic Patterns in Mesoamerica

Both 'centers of origin' and 'vicariance' hypotheses are biogeographical statements that presuppose that areas of endemism are interrelated and that these patterns are identifiable. What does it mean though to say that two areas of endemism are related to one another? We could pick on any two areas of the world and pick on any reason to say that they are biogeographically related to one another. For example, consider the southeastern states of North America and the tropical parts of Central America (Fig. 1). The fact that they have many groups of organisms in common means that they are related. But, do numbers really mean anything? We could equally pick on one endemic species from each area and say that these two are related, if only by saying that they belong to the

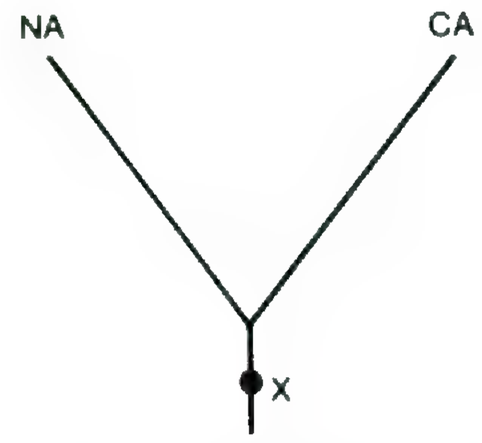

FIGURE 1. Branching diagram depicting a 2-area statement. The areas of North America and Central America are related to one another by the shared component(s) x.

same family. It is meaningless, however, to say that two areas such as North and Central America are related without some reference point to say by how much. We need, just as in statements of cladistic relationships, a minimum of three areas to express the interrelationships of two.

Consider the following example. By examining the distribution pattern of the *Acer saccharum* group (Fig. 2) there are three obvious disjunct areas—the southeastern United States (1), eastern Mexico (2), and northern Central America (3). For three such areas there are three possible ways of expressing a resolved, or fully informative relationship (Fig. 3 a, b, c).

Before it is worth answering the question of which of the three patterns is correct, it is worth answering the question does the *Acer saccharum* pattern belong to a more general pattern indicated by the three areas 1, 2 and 3? This is exactly the type of question that Croizat (1958, 1962) asked of his panbiogeographic method, and also Rosen (1975, 1978) in his studies of Caribbean biogeography. Rosen gathered a whole range of distributional data for various groups and plotted them on maps. Major disjunctions between different areas were then connected by lines or tracks. A search was then made to establish replicated or generalized tracks which indicated a common cause for the pattern. Rosen (1975) performed this type of analysis for twenty-one groups of fishes and amphibians and established that there were five major distribution tracks for Mesoamerican and Caribbean regions (Fig. 4); a North American-Caribbean track, an eastern Pacific-Caribbean track, an eastern Atlantic-western Atlantic track, and an eastern Pacific-eastern Atlantic track. The two terrestrial tracks are illustrated in Fig. 4.

Rosen (1978) showed that by examining the detailed distribution patterns of particular taxonomic groups and phylogenetic relationships, a resolved pattern of area interrelationships could be obtained. By looking at the distribution of one hundred and fourteen fish species occurring in ten river systems from the Rio Grande to the Rio Papaloapan, Rosen showed a higher probability that the areas 2 and 3 (Fig. 2) were more closely related to one another because the nominal sister group relations were congruent in the expression of such a pattern. Of the one hundred and fourteen taxa, thirty-six are endemic to the Rio Grande, none is endemic in the next two rivers south, fourteen are endemic to the Rio Panuco Basin, and thirty-five occur only in the rivers south of the Rio Panuco. Of the thirty-six in the Rio Grande, some are the same as, and others are most closely related to, species of the southeastern United States (thus showing that the Rio Grande is part of a much larger region of endemism). Of the thirty-five

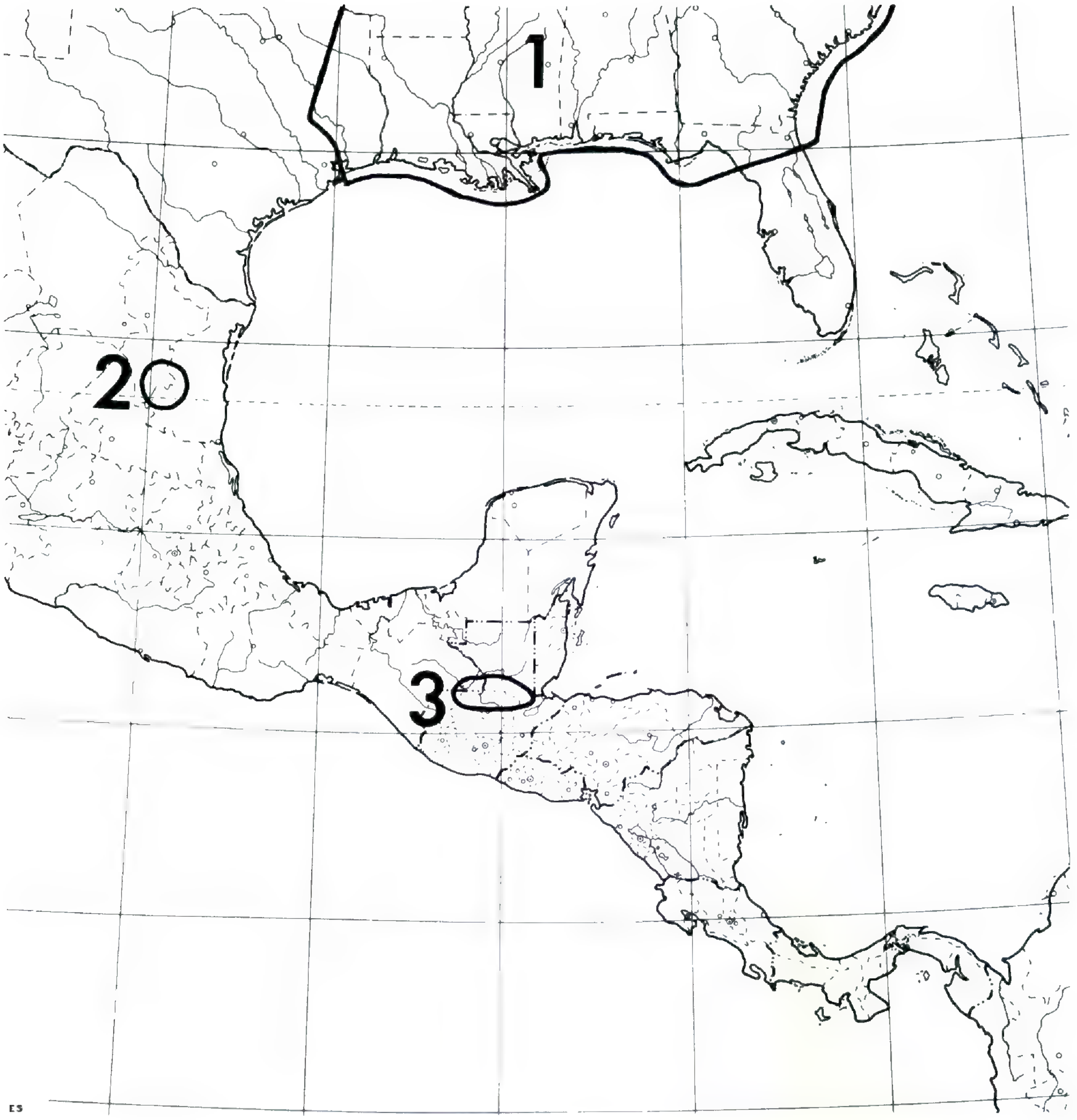

FIGURE 2. The occurrence of *Acer saccharum* group in middle and North America.

taxa in the six rivers south of the Rio Panuco, some are the same as, and others are most closely related to, species in the remainder of southeastern Mexico and northern Central America. The interrelationships of the three disjunct areas are thus defined and the patterns suggest that areas 2 and 3 are more closely related to one another than they are to area 1. For the *Acer saccharum* group the taxonomy is sufficient to resolve that areas 2 and 3 are more closely related to one another than area 1.

The question one might ask now is: what are the implications of this type of statement? The answer would be that an initial vicariance event is postulated as having occurred somewhere between the Rio Grande and the Rio Panuco Basin followed by a second, later, vicariance event dividing the Rio Panuco Basin and southern Mexico with Central America. At this level of resolution three-area

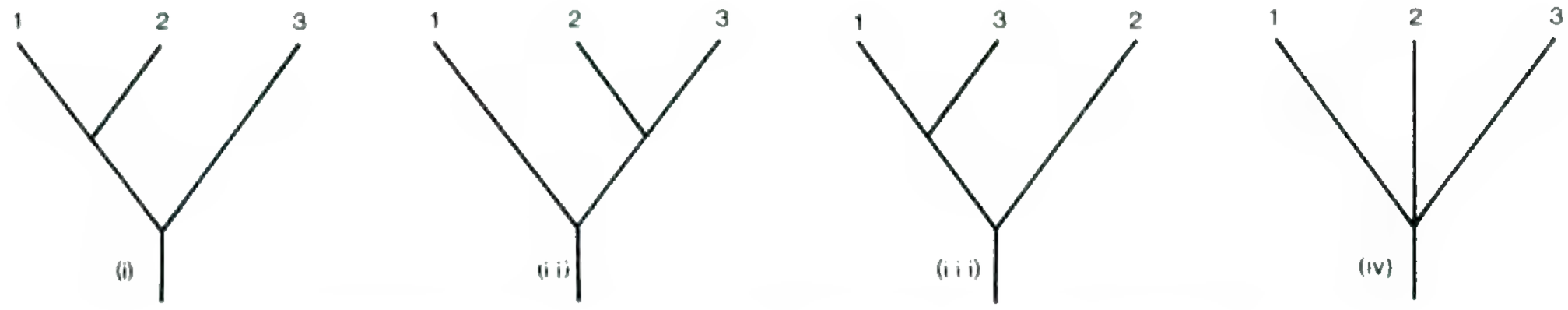

FIGURE 3. Branching diagrams to show the full range of cladistic relations for 3 areas.

cladograms give only simple answers. Despite the effort involved for producing three-area cladograms, several two-step paleogeographic events can be correlated with the cladograms to give two such obvious disjunctions. To get a much more significant result it is necessary to look at the detailed relationships of groups which occupy all or most of the identifiable endemic areas.

The detailed distribution patterns of many groups with three or more taxa are known for Mesoamerica, but detailed phylogenetic hypotheses for plant groups can be counted on one hand. Analytical biogeography is extremely demanding, ideally requiring many phylogenetic studies of widely different, randomly selected groups occupying similar areas (see Humphries, 1981). Recently published botanical cladograms include those of Judd (1981), Bolick (1981), and Sanders (1981), but the groups on which they worked to not occur in identical endemic areas and so do not make a detailed analysis possible. Rosen's (1975, 1978, 1979) work on the poeciliid fish genera *Heterandria* and *Xiphophorus* can serve as a more detailed study of groups occupying several areas and demonstrates the latest developments in analytical biogeography. Although these studies may be familiar to the botanical community, particularly through the paper and book of Wiley

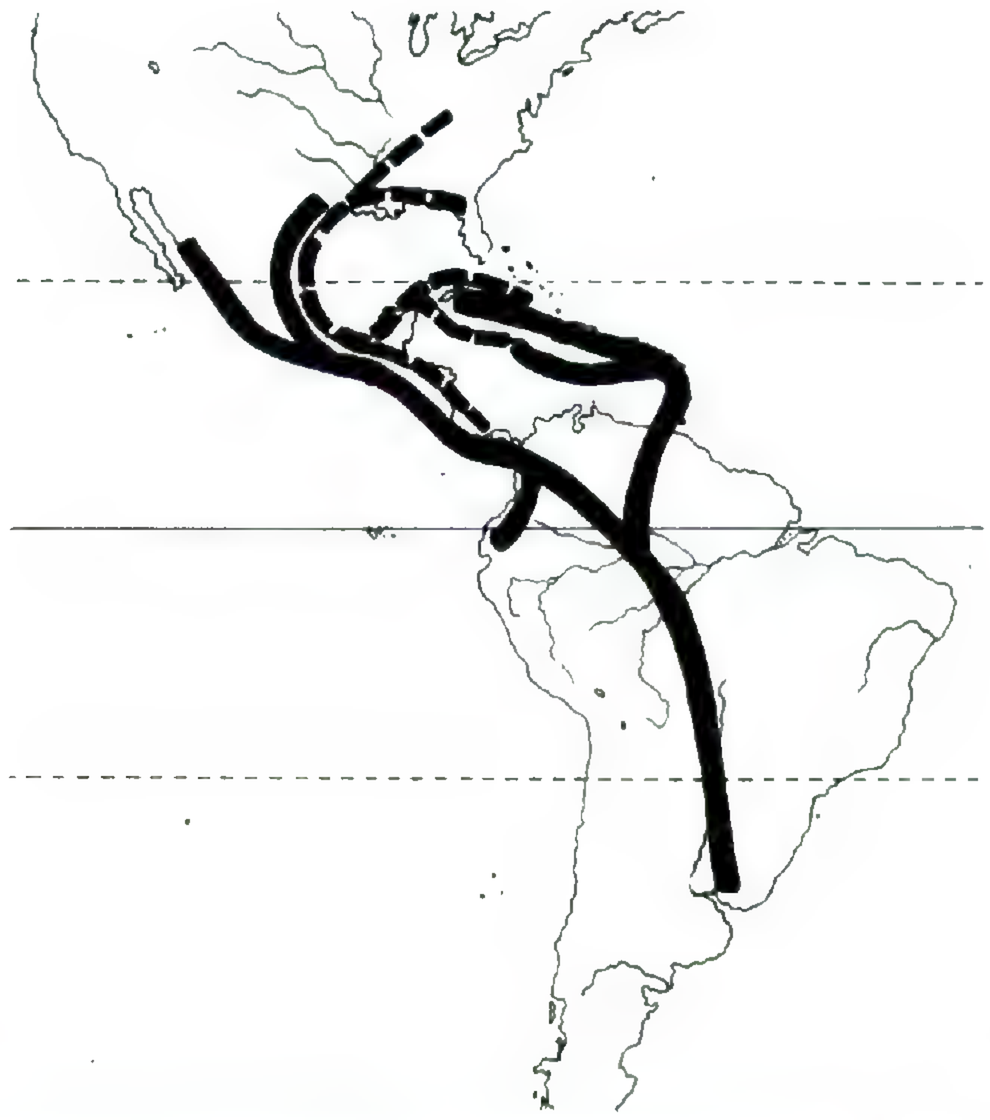

FIGURE 4. Summary of transcontinental generalized tracks. Overlapping of North and South American tracks enclosing the Caribbean sea (after Rosen, 1975, Fig. 6C).

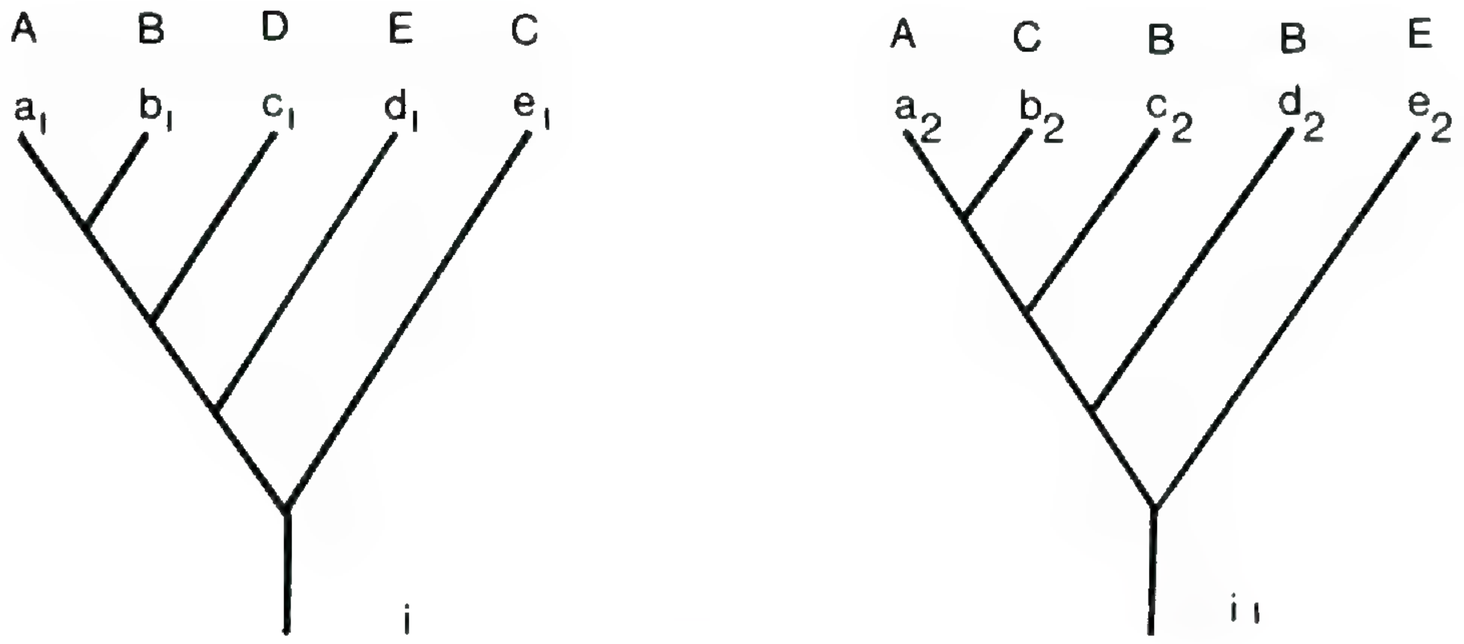

FIGURE 5. i, ii. A comparison of two area cladograms. iii. Reduced consensus cladogram showing common components to cladograms i and ii.

(1980, 1981), they have been undertaken under restrictive assumptions (Platnick, 1981) and are thus worthy of another consideration, since they still remain the only fully worked examples for the areas of our concern.

TRANSFORMING DATA—A THEORETICAL ASIDE ON COMBINING CLADOGRAMS

Before considering the explicit examples of *Heterandria* and *Xiphophorus*, it is necessary to consider the notion of compatibility or congruence between cladograms in more detail. To search for congruence between different cladograms occupying similar areas, the taxa are substituted by area notations to give area cladograms (Rosen, 1975, 1978, 1979). If, when compared, several phylogenies match one another, we can, as seen earlier, hypothesize that congruence is due to a common history. However the success with which we find congruence is reduced by the number of unique patterns affecting the distribution and origin of each group of organisms. In other words, when several groups are compared and show incongruent patterns they might still have had similar evolutionary histories. Apparent incongruences might be due to a number of factors giving incongruent and unresolved patterns in the original taxonomy, all of which can give errors in interpretation of their meaning. To overcome these problems we cannot resort to interpretations of evolutionary process, but we can use only the logic of cladograms and develop ways of adding cladograms together to given us general area statements (see Nelson & Platnick, 1981). So far two main methods for dealing with incongruences have been described, Rosen's method of reduced area cladograms and Nelson and Platnick's method of component analysis, although Mickovitch's transformation series analysis might be yet another technique.

1. ROSEN'S METHOD OF REDUCED AREA CLADOGRAMS

The technique of reduced area cladograms was put into practice by Rosen (1978). It is designed to find a common pattern for the areas of two or more different groups of taxa by eliminating unique or incongruent elements from the individual groups. Consider the two cladograms in Fig. 5 i, ii. In the first group the five taxa a, b, c, d, e occur in five areas A, B, C, D, and E. In the second group the five taxa a, b, c, d, and e occur in four areas A, B, C, and E. Area D

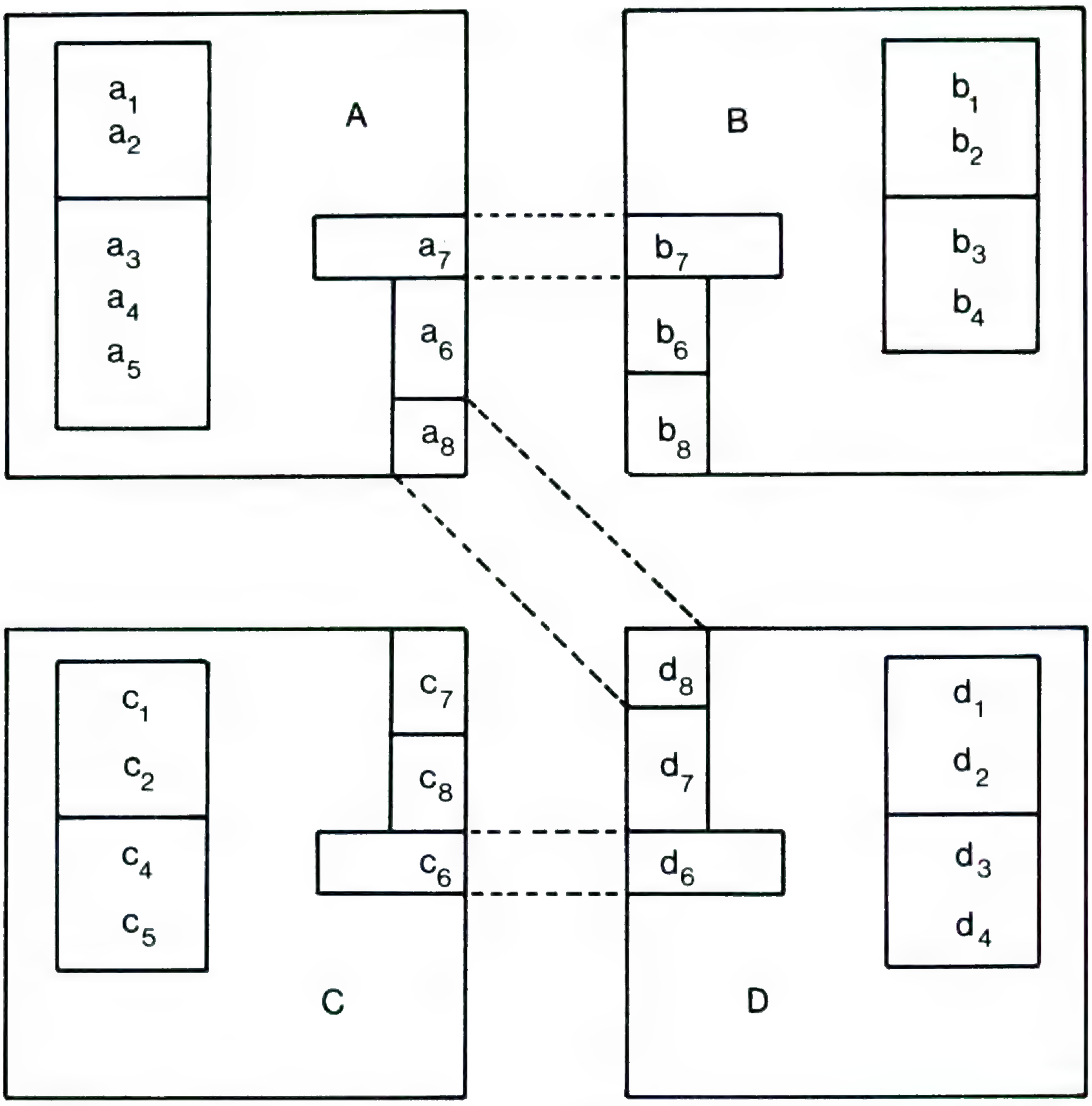

FIGURE 6. Hypothetical map for four areas ABCD, and the hypothetical distribution of eight taxonomic groups, $a_1\ b_1\ c_1\ d_1$, $a_2\ b_2\ c_2\ d_2$, $a_3\ b_3\ d_3$, $a_4\ c_4\ d_4$, $a_5\ b_5\ c_5$, $a_6\ b_6\ cd_6$, $ab_7\ c_7\ d_7$, $ad_8\ b_8\ c_8$.

is unique to the first cladogram and so is considered to be uninformative. Area C occurs in different positions on the two cladograms and is thus considered to be incongruent. Since area B is only a single area in geographical terms its appearances for both taxa, c and d, in the second cladogram can be reduced to a single terminal statement in the consensus cladogram (Fig. 5 iii). The consensus cladogram produces a statement of those areas, A, B, and E, which share a common history.

2. NELSON'S AND PLATNICK'S METHOD—COMPONENT ANALYSIS

For the purposes of discussion consider four hypothetical areas ABCD and the hypothetical distribution of eight different hypothetical groups of taxa, labelled for the sake of convenience 1–8 (Fig. 6, Table 1). The first two groups of taxa, numbered abcd 1 and 2, each have one endemic in each of the four areas of

TABLE 1. The distribution of eight groups of taxa in four areas—see Fig. 6 and text for explanation.

A	B	C	D	Areas
a_1	b_1	c_1	d_1	one endemic in each area
a_2	b_2	c_2	d_2	
a_3	b_3	*	d_3	one extinction in each area
a_4	*	c_4	d_4	
a_5	b_5	c_5	*	
a_6	b_6	(cd_6)		one widespread taxon in two areas
(ab_7)		c_7	d_7	
ad_8	b_8	9_8	ad_8	

our concern. The second group of taxa, numbered abcd 3, 4, and 5, and have less than ideal distributions since they have one missing taxon from each of the areas of our concern. The third group of taxa numbered also have less than ideal distributions since each group has three taxa with a widespread species occurring in two of the four areas.

In the first example, involving the first two groups of taxa, the geological hypothesis (Fig. 7) indicates that the areas AB are more closely related to one another than they are to either C or D and at some relatively earlier point in time the areas ABC were more closely related to one another than to the fourth area D. The two biological cladograms are perfect in the sense that they have endemic taxa in each of the four areas and the cladograms indicate complete resolution of their relationships. They show complete congruence with the geological cladogram and yield only the same area components as indicated in Fig. 7 i–iii by the numbered black dots next to the branch points.

The second example shows the problem of how to obtain information about the interrelationships of areas in the absence of geological cladograms and with imperfect cladograms, since each has a different endemic missing from one of the areas (Fig. 8 i–iii). Looking at all three cladograms individually there is a range of different area components (see Fig. 8 i–iii, 0–5). Thus Fig. 8 i has two components, labelled 0 and 3, Fig. 8 ii has two components labelled 4 and 5 and Fig. 8 iii shows two components labelled 2 and 3.

Since each cladogram has only three terms (i.e., terminal taxa), they have only two rather than the requisite three components to identify the relationships of four areas. In other words they each lack the fourth area, ABCD, component 1. Also, if we assume that the relationships of the three groups of organisms are the result of similar historical causes then two of the apparent components in the array given by the the three cladograms (Fig. 8 i–iii) must be false since only two can be true to give a fully resolved cladogram of four areas. As each cladogram has three of the four terms required, the missing term can be added. As shown in Fig. 9 the missing term can be added in one of five different places. Since for any one cladogram we do not know where to add the missing term, this means that we have five possible results for the interrelationships of areas. For example, consider the cladogram in Fig. 8 i. By adding the missing C term the five fully restored cladograms can be seen in Fig. 9 i–v. Similarly, for the cladogram shown in Fig. 8 ii the missing B term can be added as shown in Fig. 9 i, iii, iv, vii, ix

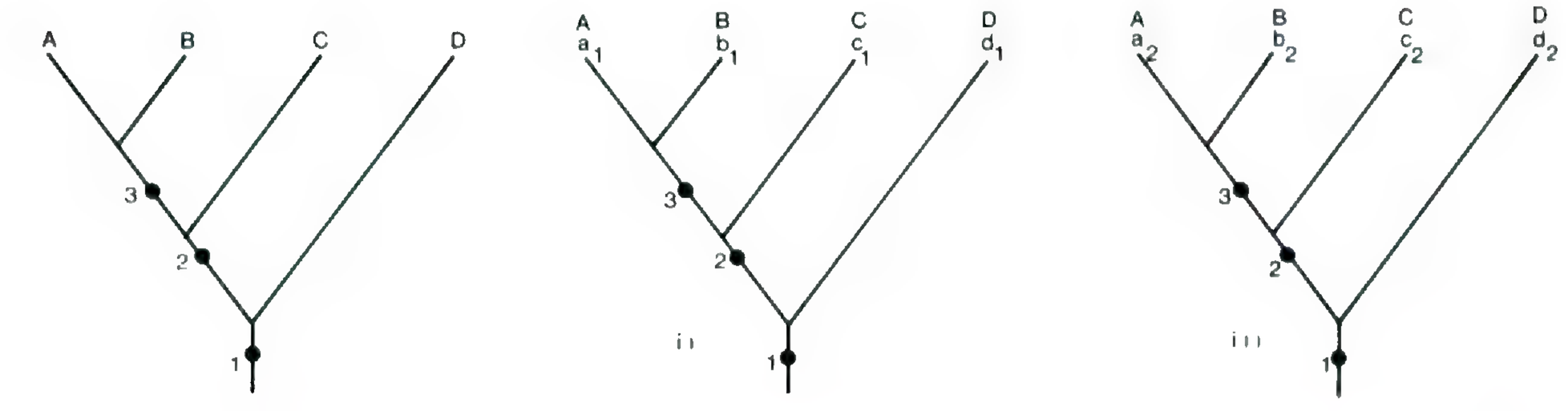

FIGURE 7. Hypothetical area cladograms. (i) cladogram for four areas ABCD defined by three components 1, 2, and 3 (ii) + (iii) cladogram for two groups of four taxa a_1 b_1 c_1 d_1 and a_2 b_2 c_2 d_2 and the areas in which they occur also specified by 3 components 1, 2, and 3 (see text for explanation).

and similarly for the cladogram shown in Fig. 8 iii the missing D term can be added as shown in Fig. 9 i, ii, v, vi, viii. In other words, of the fifteen possible cladograms, eight of them, representing more than 50% of the total, are reiterated. Four of the complete cladograms (Fig. 9 vi–ix) account for only one of the partial cladograms. Similarly, four of them account for two of the partial cladograms (Fig. 9 ii–v) and only one (Fig. 9 i) actually accounts for all three of the partial cladograms. Thus, if the patterns of the three partial 3-taxon cladograms are due to common history, then the only information in them about the interrelationships of the four areas is the cladogram in Fig. 9 i, which must be the correct one. This cladogram identifies the components 1, 2, and 3 as real and the components 0, 4, and 5 as misleading due to missing information. But assuming all of the original components as real is a problem since when they are added together they give a

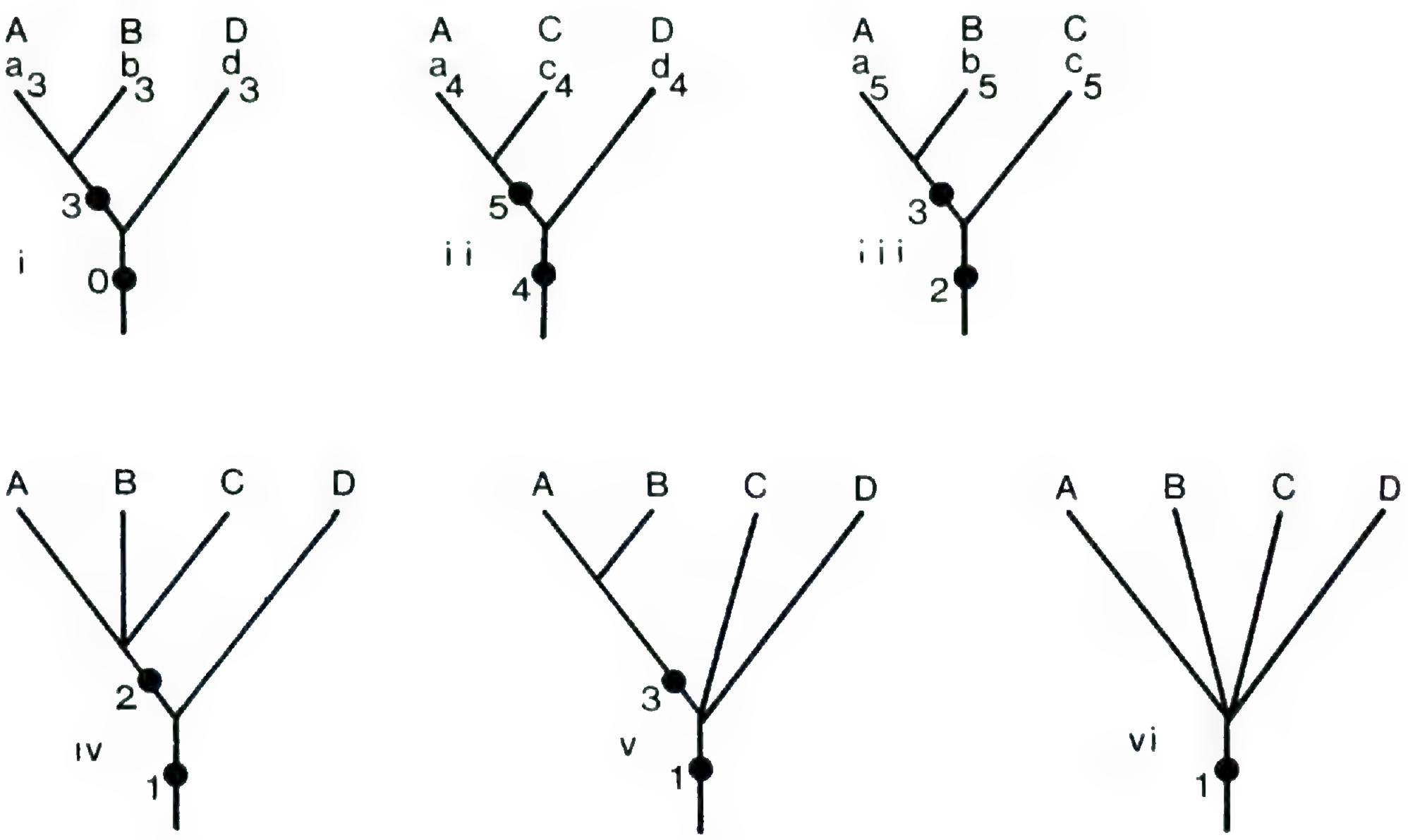

FIGURE 8. Hypothetical area cladograms for three groups of three taxa, a_3 b_3 d_3, a_4 c_4 d_4, a_5 b_5 c_5, (i, ii, & iii) occurring in four areas; (iv), (v), and (vi) generalized area cladograms obtained by adding together cladograms i + ii, ii + iii, and i + ii + iii respectively (see text for explanation).

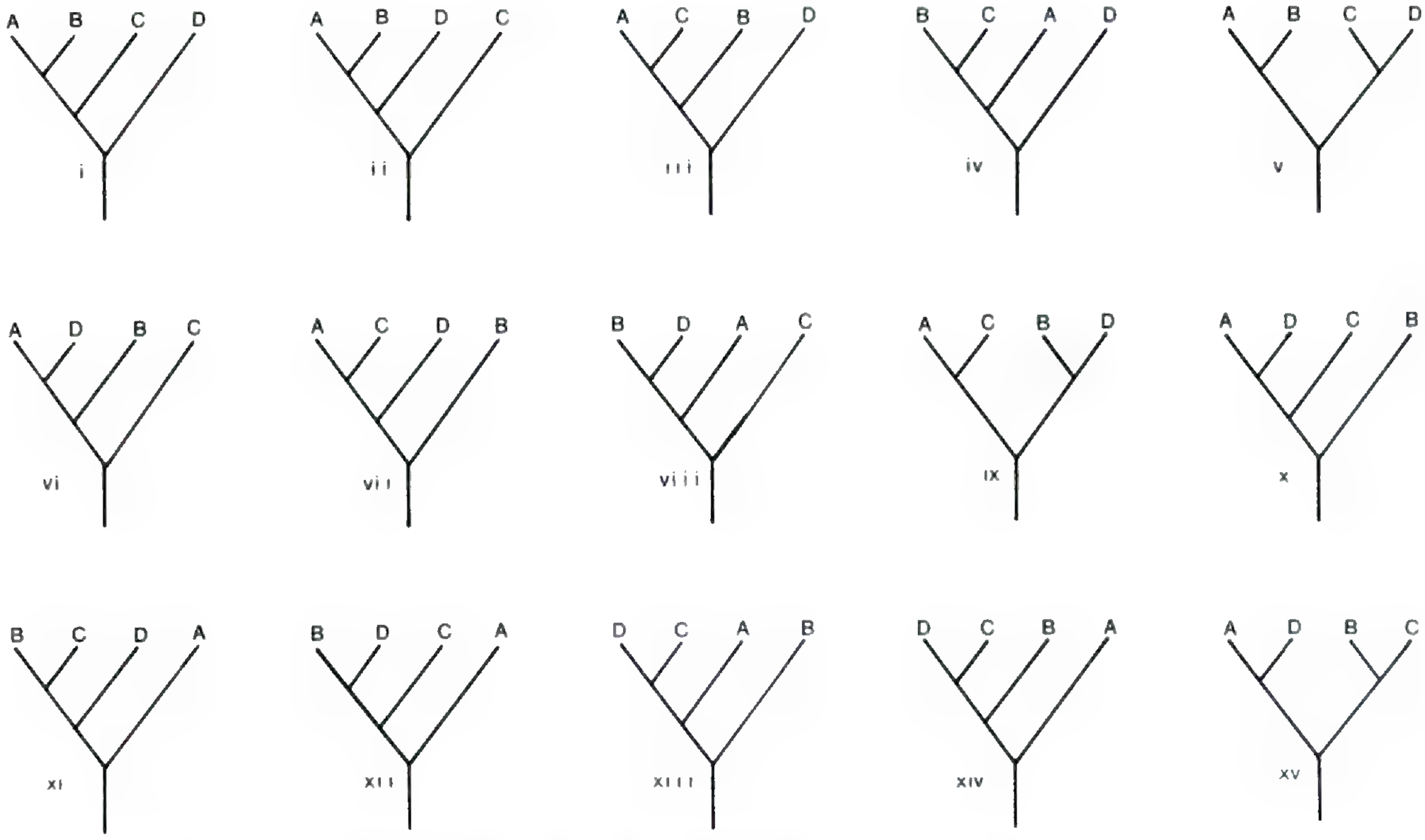

FIGURE 9. The fifteen possible resolved cladograms for four areas.

totally uninformative answer. By adding the cladograms in Fig. 8 i and ii together the ABCD component 1 is recovered but there is no way of resolving the AB and AC components, 3 and 5, and thus the ABC component must be left as an unresolved trichotomy (Fig. 8 iv). Similarly, by adding the cladograms in Fig. 8 i and iii together, the AB component 3 and the ABCD component 1 are both recovered but the incongruency for the 0 and 2 components leaves the AB, C, and D areas as an unresolved basal trichotomy (Fig. 8 ii). When all three of the partial cladograms are added together a totally uninformative result is obtained except for the recovery of component 1 (Fig. 8 vi).

In the third group of taxa the cladograms are characterized by each having species in all four areas but one in each of the three cladograms has one widespread species occurring in two of the areas (Figs. 10 i, ii; 11 i, ii; 12 i, ii). A comparison of the area cladograms indicates that each is less than fully informative since the widespread species give effectively unresolved area interrelationships. As was seen to some extent in the second example (Figs. 8 and 9), missing endemics can be considered under two different assumptions. Under the first assumption all of the components can be considered as informative, but under the second we can allow for missing information and apply the full cladistic logic by admitting that some of the components are false. The theoretical ramifications of assumptions one and two have been discussed at length by Nelson and Platnick (1981).

Under assumption one whatever is true of a widespread taxon (see taxon cd6 in Fig. 10 i) in one part of its range (area C, Fig. 10 ii) must also be true of the taxon in other parts of its range (area D, Fig. 10 ii). However, under assumption two whatever is true of the widespread taxon in one part of its range need not also be true of the taxon elsewhere. The implications are that under assumption

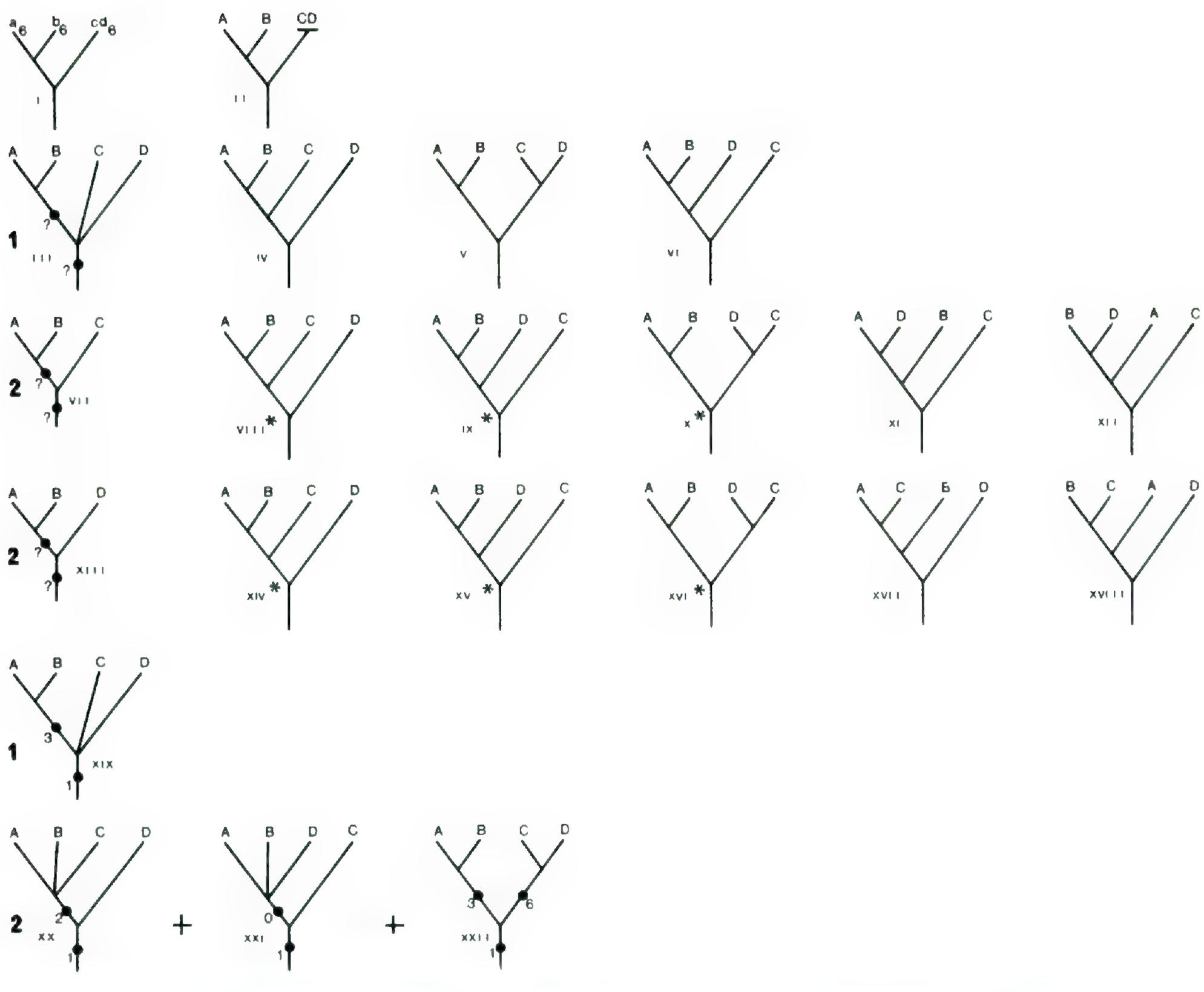

FIGURE 10. Component analysis for three taxa a_6 b_6 cd_6 (i) expressing a mixture of endemic, i.e., 1 and 2 in A and B, and widespread distributions 3 in CD (ii); (iii–vi) component analysis under assumption 1; (vii–xviii) component analysis under assumption 2; (xix) summary components under assumption 1; (xx–xxii) summary components under assumption 2. See text for explanation.

one the taxon occupying area CD will never be split into separate taxa. More precisely, if species b6 in area B and species a6 in area A are more closely related to each other than to species cd6 in area C then species b6 and a6 are also more closely related to one another than they are to species cd6 in area D. Under this assumption the area cladogram (Fig. 10 iii) yields a single within-group component (3 in Fig. 10 xix). Such a partially resolved cladogram would, under further analysis, allow for only three fully dichotomous cladograms (Fig. 10 iv–vi). Under assumption two the CD occurrences of taxon cd6 might at some time be divided into two separate entities, such that whatever is true of one occurrence might not be true of another. Using the same example, if species a6 in area A and species b6 in area B are more closely related between themselves than to species cd6, the relationship might only be true for species cd6 in area C, or, for species cd6 in area D, but not for both. Under this assumption the area cladogram yields two possibilities for component analysis (Fig. 10 vii, xiii) but each possibility includes only three of the four areas under consideration. The two components ABC and ABD each allow for five different, fully dichotomous cladograms when

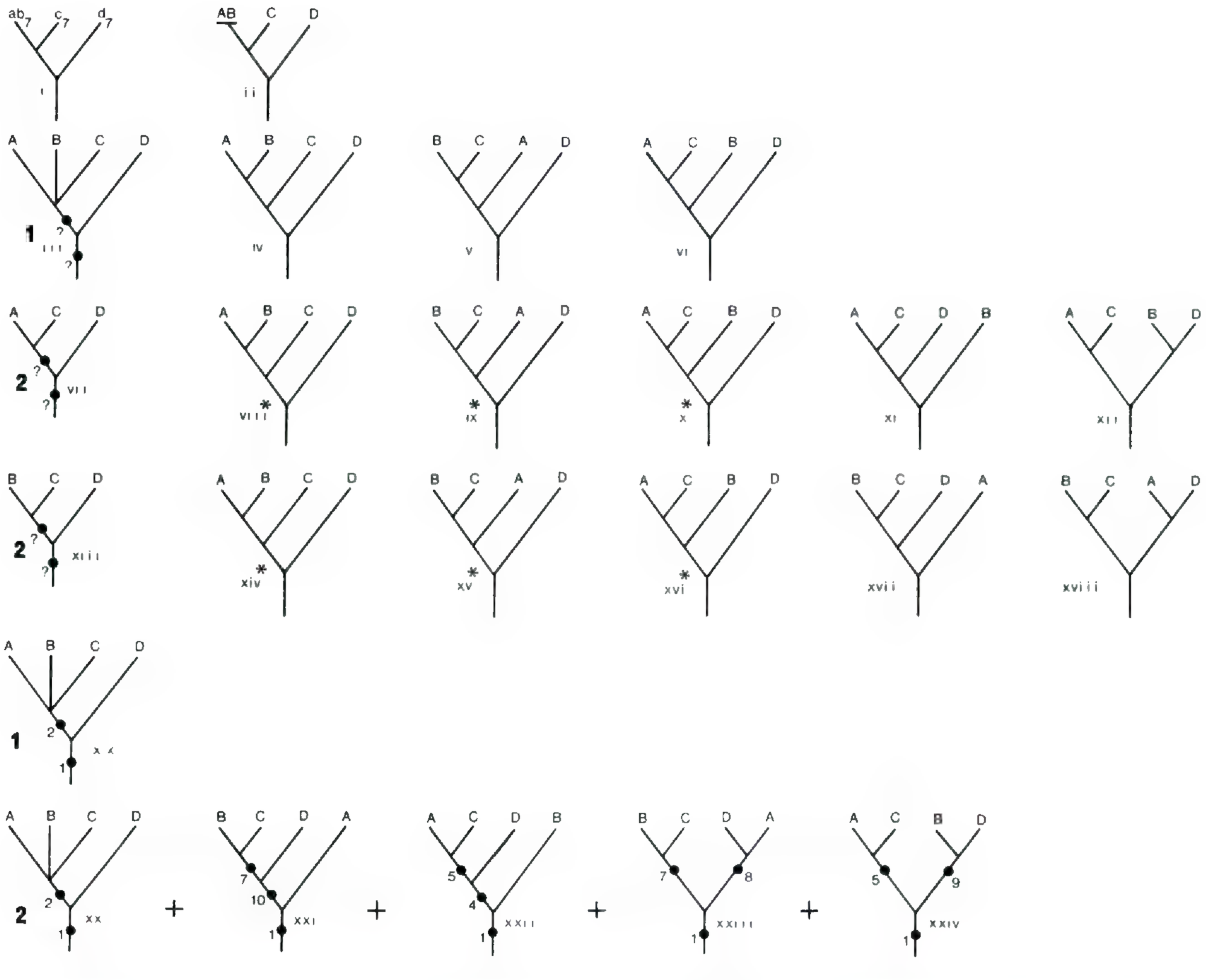

FIGURE 11. Component analysis for three taxa ab_7 c_7 d_7 (i) expressing a mixture of endemic, i.e., c_7 and d_7 in C and D, and widespread distributions ab_7 in AB (ii); (iii–vi) component analysis under assumption 1; (vii–xviii) component analysis under assumption 2; (xix) summary of components under assumption 1; (xx–xxiv) summary of components analyzed under assumption 2. See text for details.

the missing D and C terms are added (Fig. 10 viii–xii, xiv–xviii). A comparison of the two rows of cladograms shows that three in each are repeated (as shown by the asterisks) giving a total of seven different cladograms for the two component analyses. These results differ from assumption one by resolving four components within the ABCD group but there is conflict between components 0 and 2 (Fig. 10 xx–xxii).

Similar analyses have been carried out on two other species cladograms (Figs. 11, 12) but with the widespread species in different positions on the cladogram. Under assumption one there are three possible cladograms which, when combined together, yield two components within each group (Figs. 11; 12 iii–vi; xix, components 1 and 0). Under assumption two (Figs. 11; 12 vii–xviii) there are again seven possible different cladograms for each analysis. The summary cladograms (Figs. 11; 12 xx–xxiv) yield five different possibilities.

Combining the different area cladograms to give single general area cladograms (see Figs. 13, 14) is equivalent to combining together the implied summary cladograms of the component analyses which give the most likely solutions. For

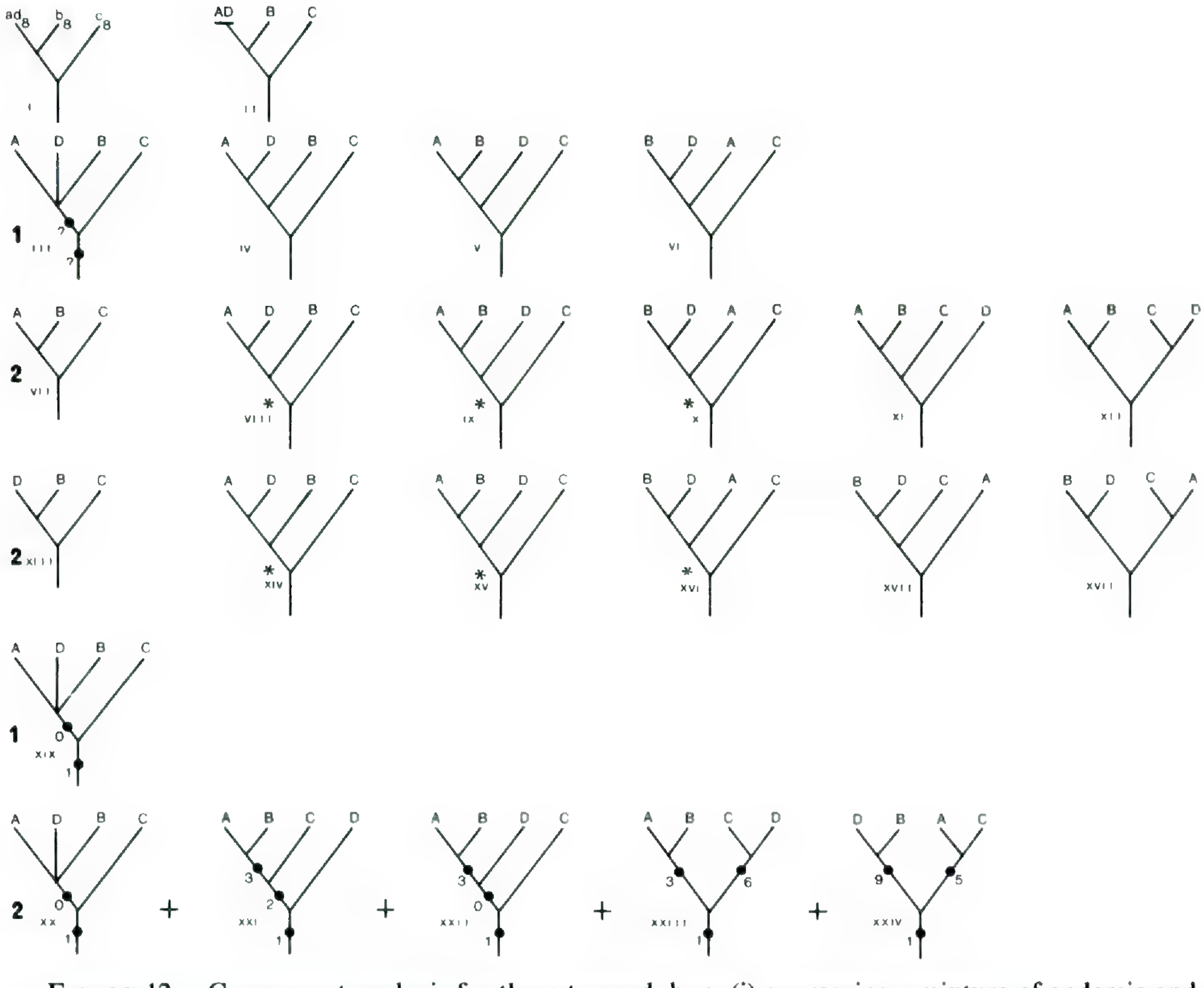

FIGURE 12. Component analysis for three taxa ad_8 b_8 c_8 (i) expressing a mixture of endemic and widespread distributions (ii); (iii–vi) component analysis under assumption 1; (vii–xviii) component analysis under assumption 2; (xix) summary of components analyzed under assumption 1; (xx–xxiv) summary of components analyzed under assumption 2. See text for details.

example, suppose we had the two area cladograms for the two species groups 6 and 8 (Figs. 10 and 12 i, ii). Under assumption one (Fig. 13 iii–v) combining the two cladograms would give two conflicting components, 0 and 3, and an uninformative consensus cladogram. Under assumption two there are several possibilities of which just two are shown (Fig. 13 vi–xi). For example take the implied summary cladogram in Fig. 13 vi (= Fig. 10 xx). The only cladogram with which it can be combined to give an informative result is that shown in Fig. 13 vii (= Fig. 12 xxi). However, the same is true for the implied cladograms of Fig. 13 ix (= Fig. 10 xxi) and Fig. 13 x (= Fig. 12 xxii). This means that when a small number of different groups are examined there is some ambiguity about the analyses under the second assumption. However, when all three area cladograms containing the widespread species are combined (Fig. 14) only one fully informative cladogram can be obtained (Fig. 14 xi), derived from the three implied cladograms shown in Figs. 10 xx; 11 xx; 12 xxi. Combining the three cladograms together under assumption one is totally uninformative (Fig. 14 iv–vii).

It must be mentioned that combining the component analyses for the species groups 6 and 7 under assumption one is totally informative (Fig. 14 xii–xiv) and

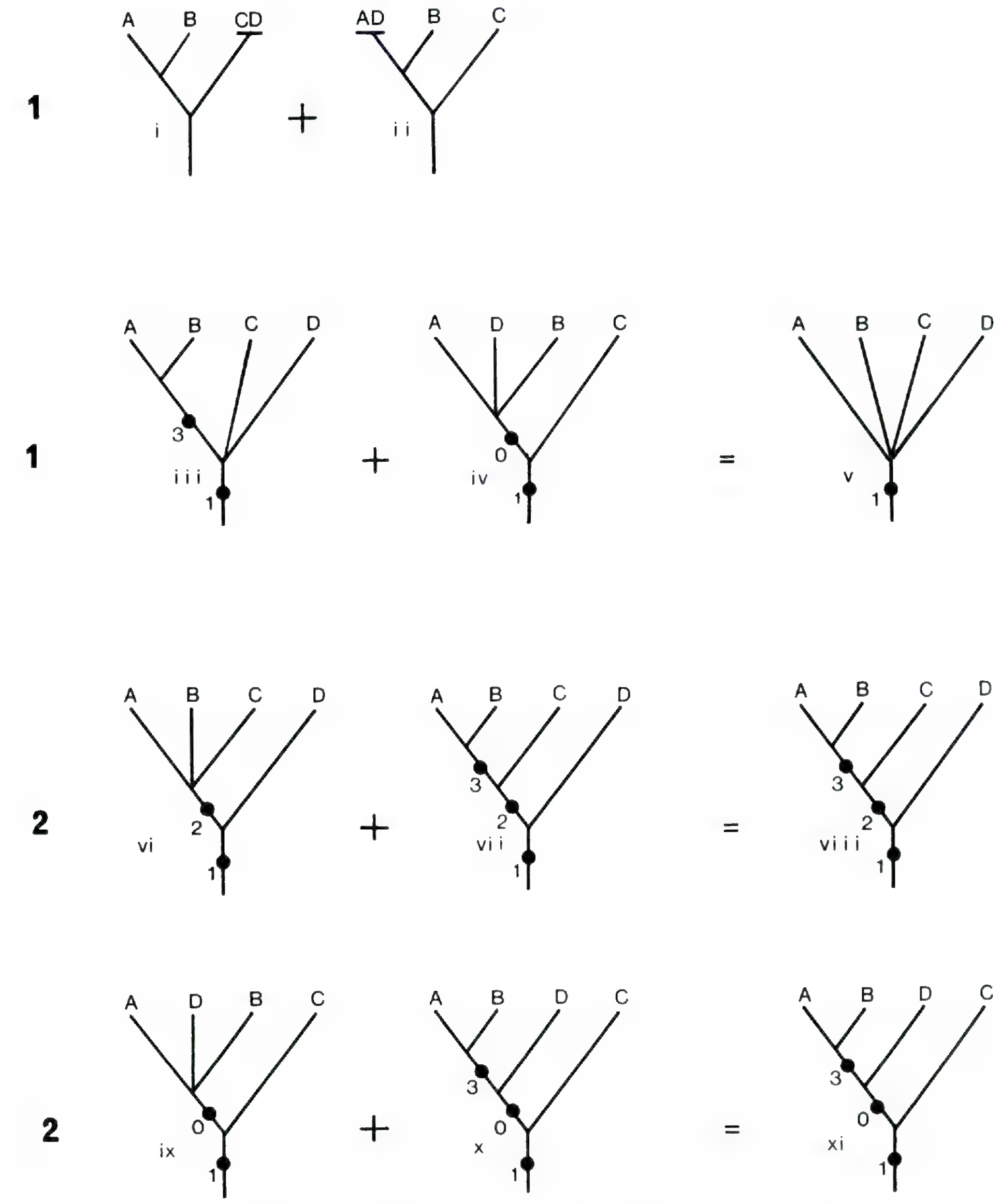

FIGURE 13. Combining components from two species/area cladograms containing widespread taxa to obtain general area cladograms; (i) cladogram from Fig. 10; (ii) cladogram from Fig. 12; (iii–v) combination under assumption 1; (vi–xi) possible combinations under assumption 2. See text for details.

only partially resolved under assumption two (Fig. 14 xv–xvii). This phenomenon occurs only when there is no overlap or conflict in the original data. The overall message from comparing the two different approaches is that assumption two is far less restrictive than assumption one. If there is any information that can be obtained from area cladograms containing ambiguous data, then it is most likely to be extracted by using assumption two.

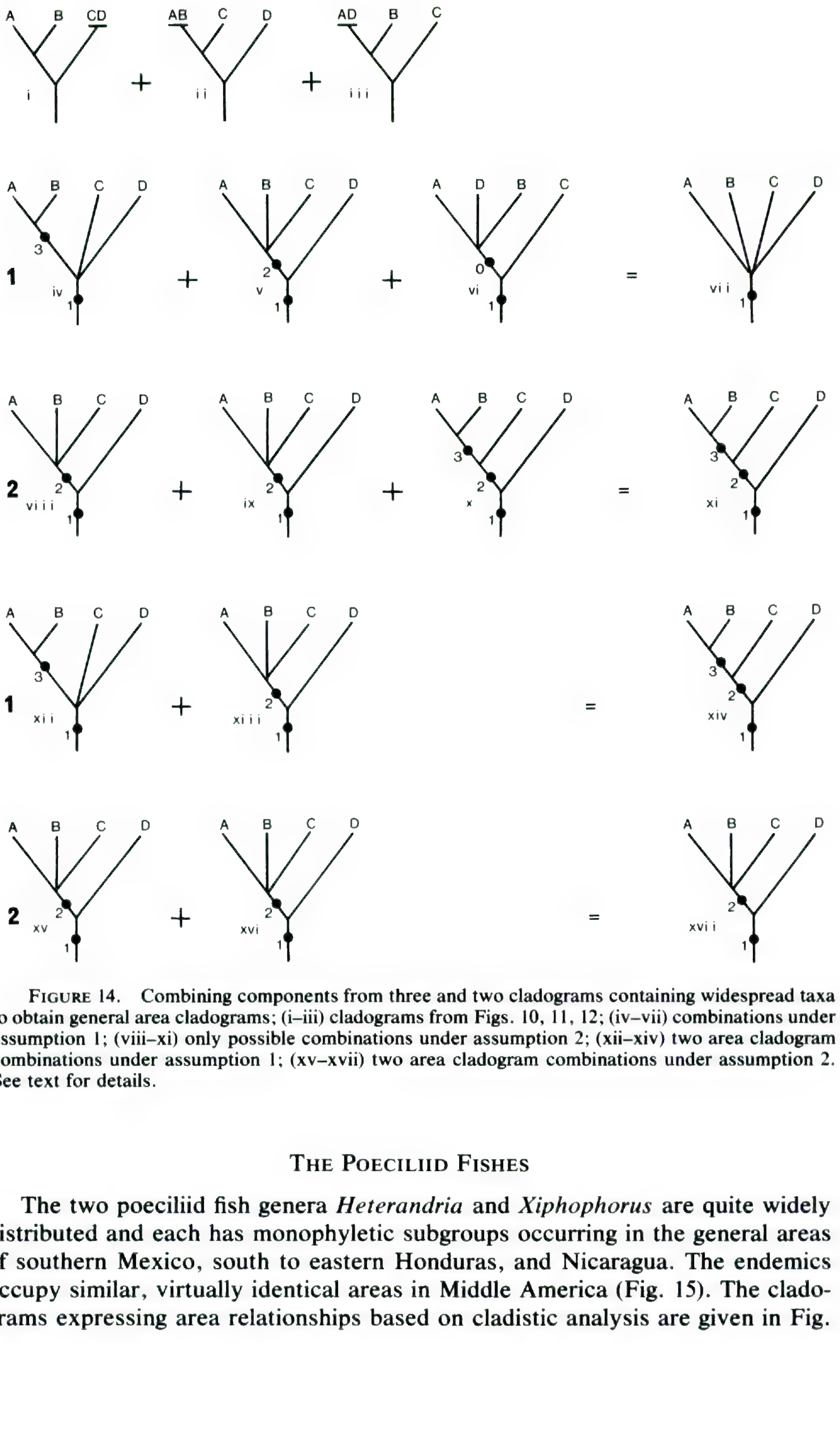

FIGURE 14. Combining components from three and two cladograms containing widespread taxa to obtain general area cladograms; (i–iii) cladograms from Figs. 10, 11, 12; (iv–vii) combinations under assumption 1; (viii–xi) only possible combinations under assumption 2; (xii–xiv) two area cladogram combinations under assumption 1; (xv–xvii) two area cladogram combinations under assumption 2. See text for details.

THE POECILIID FISHES

The two poeciliid fish genera *Heterandria* and *Xiphophorus* are quite widely distributed and each has monophyletic subgroups occurring in the general areas of southern Mexico, south to eastern Honduras, and Nicaragua. The endemics occupy similar, virtually identical areas in Middle America (Fig. 15). The cladograms expressing area relationships based on cladistic analysis are given in Fig.

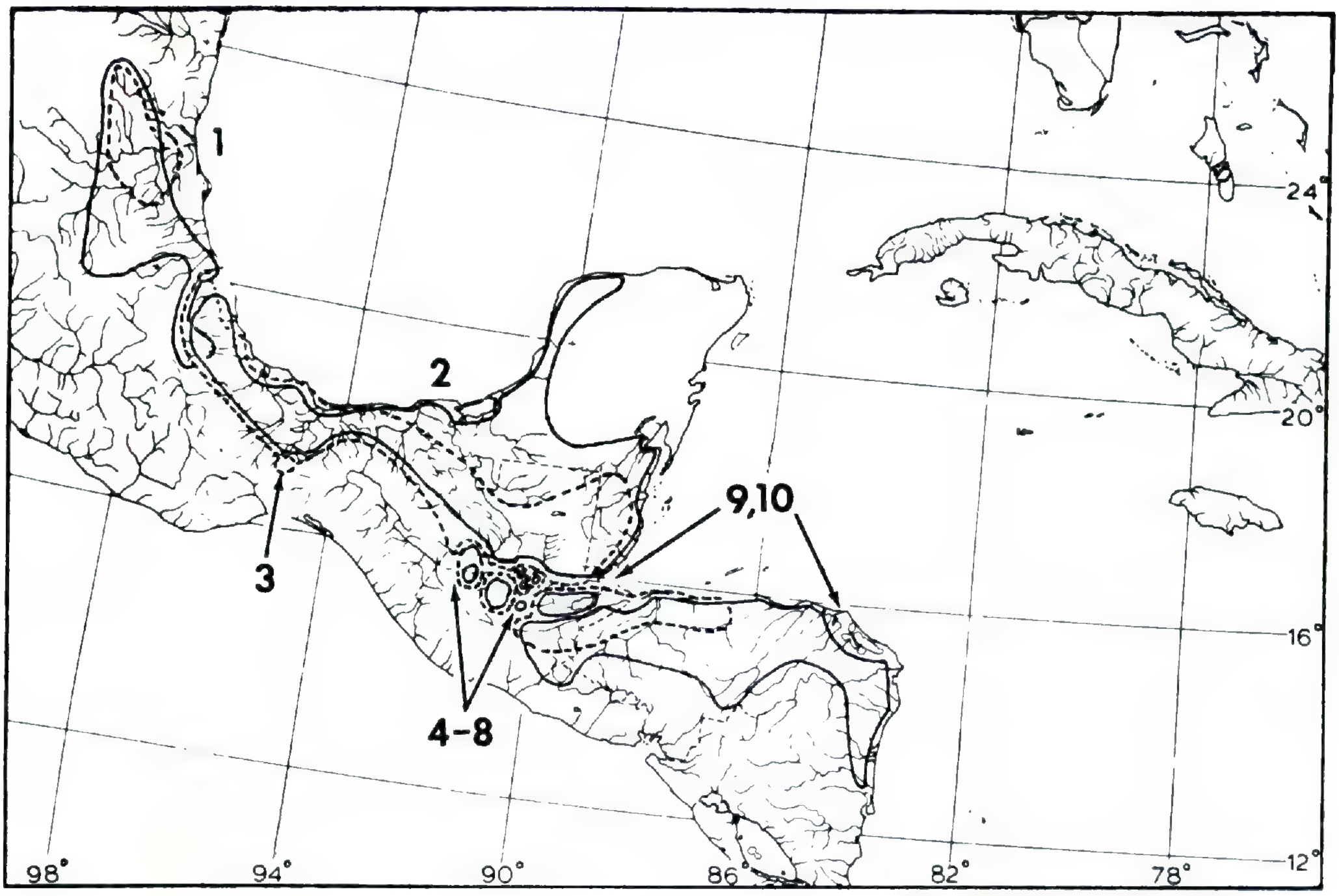

FIGURE 15. Co-occurrences of the middle American species and recognizable populations of *Heterandria* (solid) and the swordtail species of *Xiphophorus* (dashed) within 10 subregions (after Rosen, 1978, fig. 16).

16 (after Rosen, 1978, 1979; Platnick, 1981). The maps and cladograms show that there are eleven identifiable disjunct areas occupied by both species groups. Areas 4 and 5 are occupied by one species in each group and are thus treated as a single area 45. Area 11 was treated by Rosen (1978, 1979) as a hybrid area, but since it is a true disjunct area it is maintained here. Bridging taxa and hybrids have no

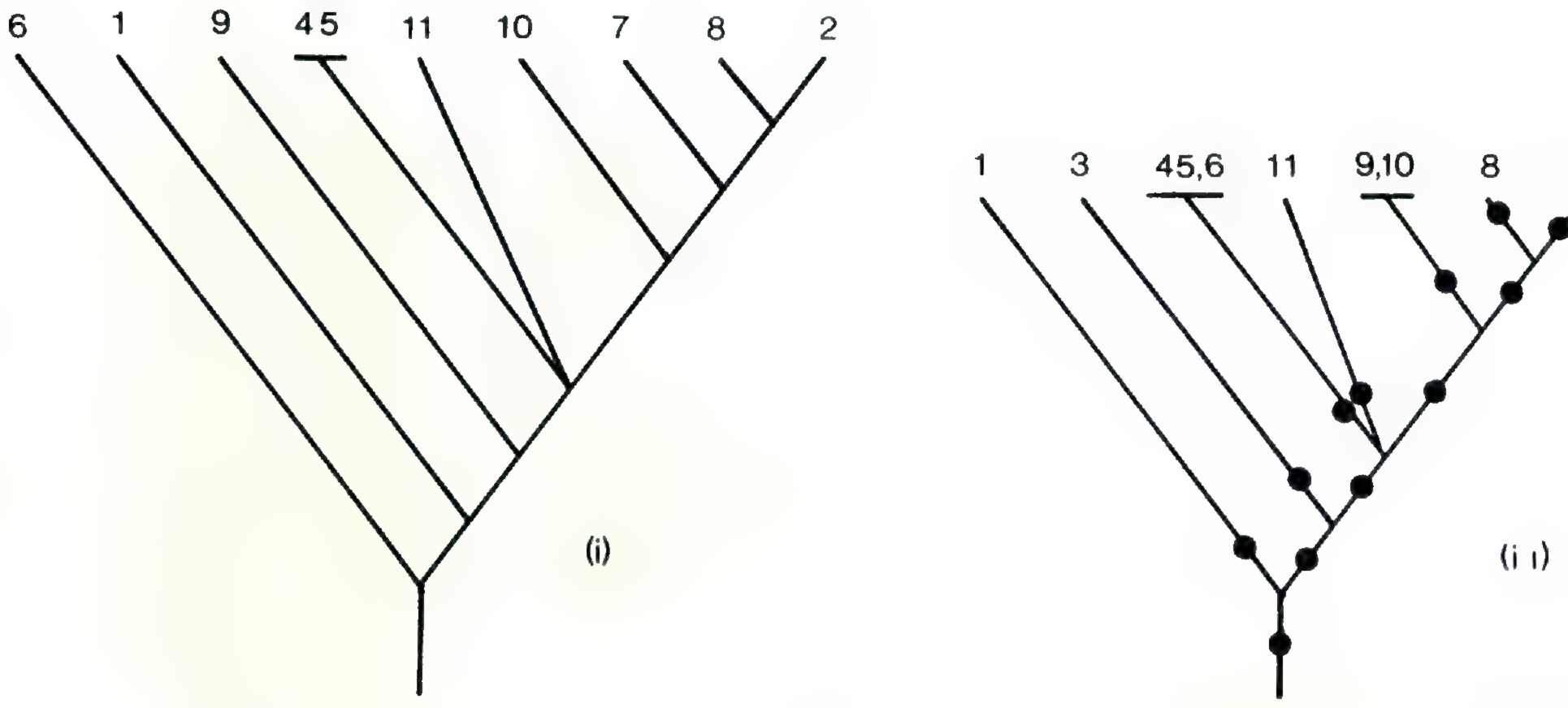

FIGURE 16. Resolved area cladograms for *Heterandria* (i) and *Xiphophorus* (ii) eliminating reticulations (after Platnick, 1981, Figs. 3–6).

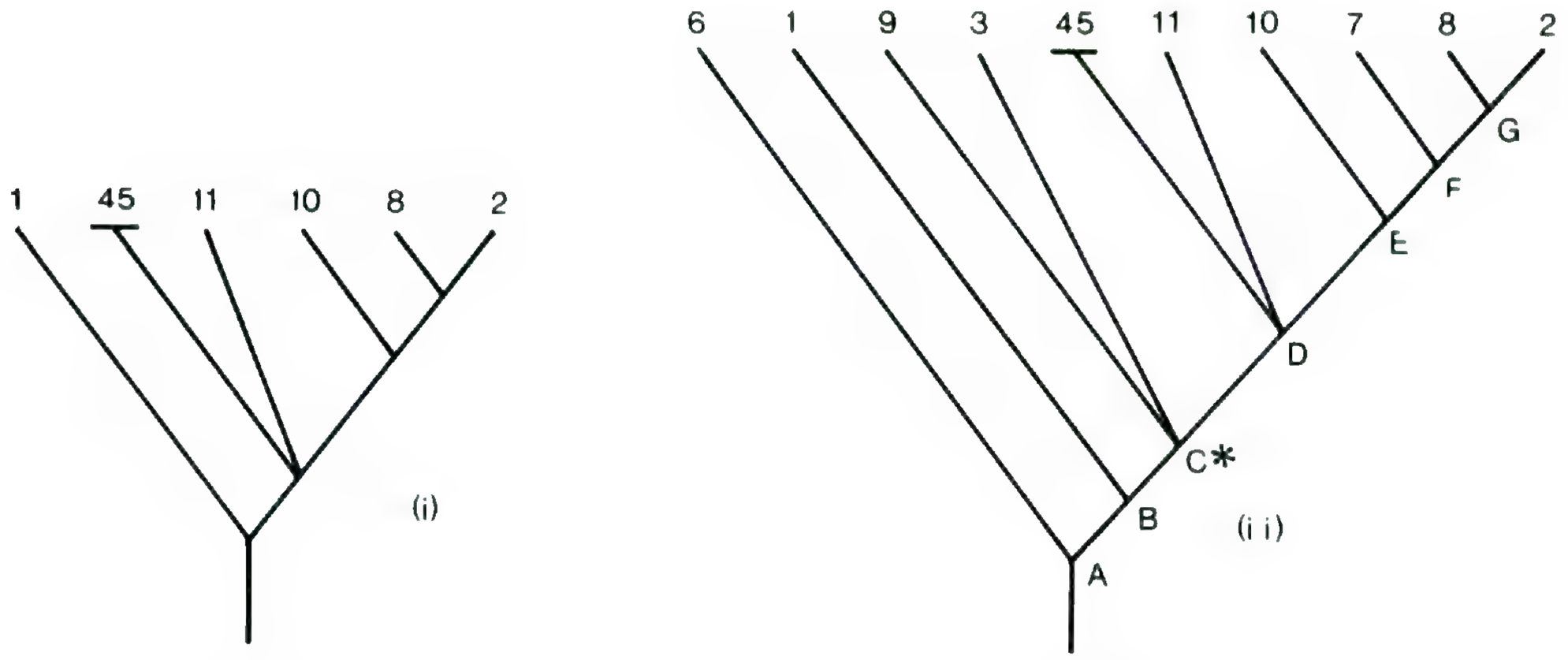

FIGURE 17. (i) Reduced general area cladogram for *Heterandria* and *Xiphophorus* analyzed under assumption 1; (ii) maximally informative cladogram for the areas occupied by *Heterandria* and *Xiphophorus* analyzed under assumption 2 (after Platnick, 1981). For key to letters and asterisk see text. Key to areas Fig. 15.

place in cladistic analysis since they are equivalent to two cladograms added together (see Nelson & Platnick, 1980, 1981). The area 11 containing ambiguous information can be treated as unresolved information and be placed at the ancestral stem.

A comparison of the two cladograms (Fig. 16) shows that *Xiphophorus* is less informative than *Heterandria* because it has two widespread species in areas 45, 6, 9, and 10 and is missing totally from area 7. In *Heterandria* areas 45, 6, 9, and 10 are all occupied by taxa.

As already shown by Platnick (1981) under assumption one whatever is true of a widespread taxon in one part of its range (e.g., *Xiphophorus alvarezi* in area 45) must also be true in another part of its range (area 6). However under as-

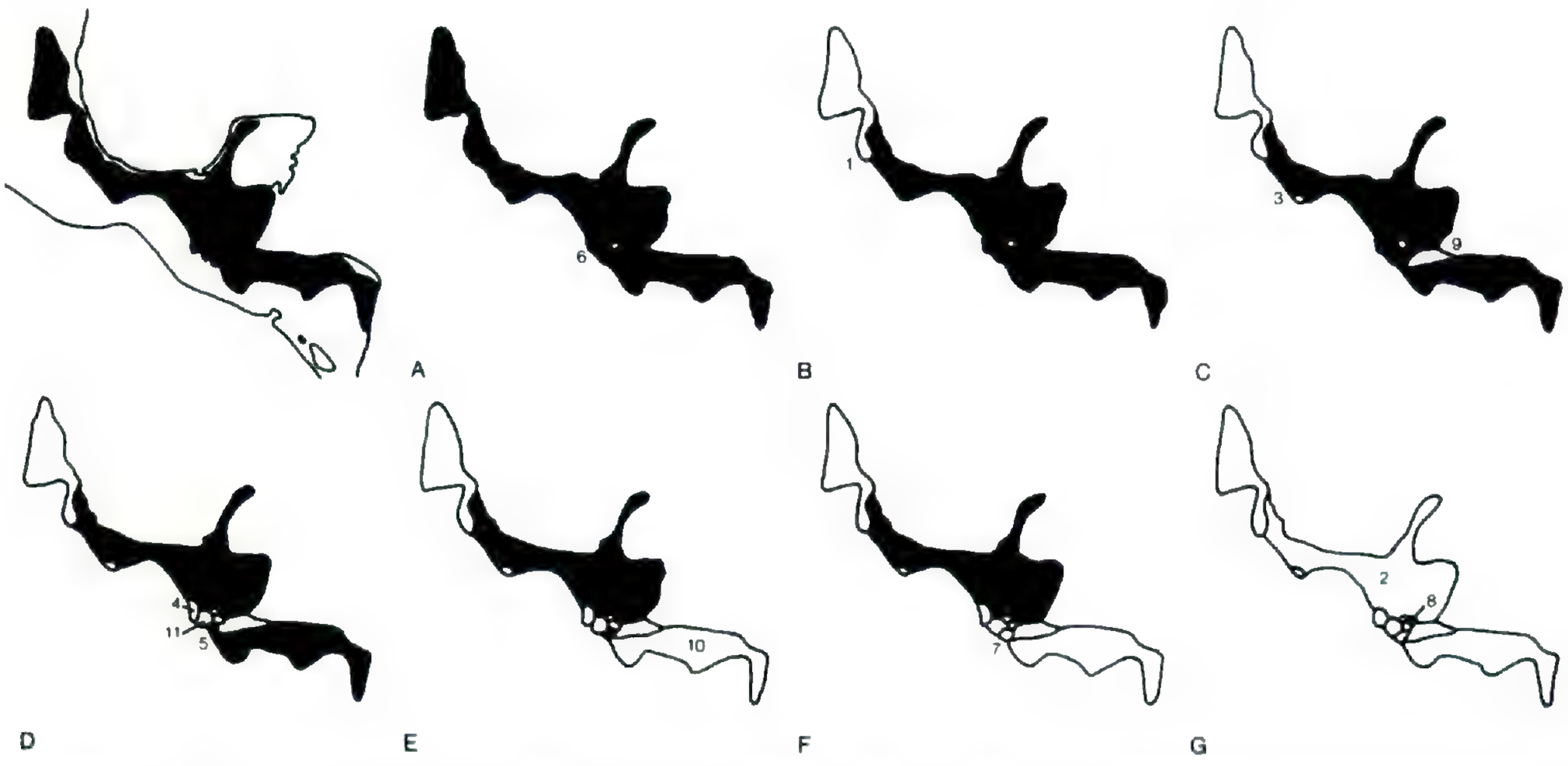

FIGURE 18. Sequence map for 11 areas in Mesoamerica when visualized through assumption 2. Letters refer to Fig. 17 ii.

sumption two whatever is true of a widespread taxon in one part of its range need not also be true of the taxon elsewhere. In other words, the widespread distributions are equivalent to saying that we are ignorant of the reasons for lack of resolution in the cladograms. In terms of distribution, that is equivalent to saying that we do not know whether the patterns are due to dispersal or a failure to speciate in response to a vicariance event. Rosen's original biogeographic method (1978, 1979) compared the two cladograms to one another and identified those parts which were congruent. Incongruent and unique areas were deleted since they were believed to be uninformative. Thus, by removing area 7, unique to *Heterandria*, and areas 3, 6 and 9, common and incongruent to both cladograms, two reduced and equal area cladograms for six areas could be produced. This is a method for obtaining a single statement for each of the congruent areas and Fig. 17 shows the result corrected for area 11. As Platnick (1981) pointed out, the removal of unique and incongruent areas is equivalent to analyzing under the first assumption. If assumption one is adopted then the *Xiphophorus* population of area 9 must be most closely related to the population in area 10, and the information for area 9 incongruent with the information from *Heterandria*. Similarly, the information on area 6 is incongruent for both cladograms.

Platnick (1981) showed that a completely different result can be obtained by applying assumption two. By taking the information on areas 6 and 9 from *Heterandria* as correct, then the incongruent information in the same areas for *Xiphophorus* is either due to dispersal or to a failure to speciate in response to a vicariance event. Rosen's original reasons for applying a version of assumption one was that such evolutionary events reduced the information content of the cladograms. Platnick (1981) noted, however, that if widespread taxa are uninformative they cannot be incongruent at the same time. Absence data can never be incongruent with the data at hand so unique areas should never be deleted. Taken on their own, widespread taxa under assumption two give uninformative components, but, when combined with other cladograms containing widespread taxa, resolved results are possible. Under assumption two the *Xiphophorus* cladogram (Fig. 16 ii) allows the populations in area 9 (or 10, but not both) and area 45 (or 6, but not both) to occur in any of twelve positions shown by black dots. The analysis yields three possible cladograms, all of which are plausible, which can be summarized by a trichotomy as shown by the asterisk in Fig. 17 iic.

The Geological Implications

Unlike the reduced area cladograms produced by Rosen (1978, 1979) and the cladogram produced here under assumption one, (Fig. 17 i), we have in Fig. 17 ii a cladogram that really does account for all eleven areas of endemism recognized from the two poeciliid fish genera. Taken from a purely vicariant point of view, the historical sequence of events for Mesoamerica that this cladogram implies is illustrated in Fig. 18. If such a pattern is due to changes in earth history, what might the historical factors have been in Mesoamerica and how might these be compared with the biological distributions? So that biotic and historical patterns can be compared we ideally would require that geological information be assembled into cladograms in the same way as biological cladograms. So far this is yet to be achieved. An examination of recent papers by Pinet (1972), Coney (this volume), Muelber-

ger and Ritchie (1975), Howarth (1981), Adams (1981), and Malfait and Dinkelman (1972) still makes it impossible to produce a geological cladogram at the same resolution as given in the most expressive combined, or even reduced, poeciliid fish cladograms (Fig. 17). However, some branch points are borne out by paleographic observations. The origin of the Gulf of Honduras occurred in the mid-Mesozoic when rifting along the Cayman trench occurred. The striking slip fault has its landward extension in Guatemala in the Motagua and Polochic faults, which probably represents the northern boundary of the Caribbean Plate. The branching pattern of the cladogram predicts that the events which isolated taxa in areas 6, 1, and 9 (Rio Candelaria, Yalicar, Rio Panuco, and Rio Polochic) preceded those which isolated the Motagua basin (area 10) and coastal Honduras drainage from North Guatemala (areas 7, 8, and 2). The region has been tectonically active ever since the Eocene (Pinet, 1972). Until such time as the geological data can be ordered for a more informative comparison, one can say little except that the observed resolved biological patterns in Mesoamerica have been formed over a period of at least 80 million years (Rosen, 1978).

CONCLUSION

Hopefully, by explaining some principles of cladistic biogeography, I've conveyed the idea that the history of organisms and the history of the earth go together. Cladistics is a general method for discovering the sub-class relations of taxa without recourse to evolutionary narrative. Cladistic biogeography is a natural offshoot from cladistics and is a general method of discovering the sub-class relations of areas by analysis of biological cladograms, again without any recourse to evolutionary narrative. By reconsidering Rosen's studies (1975, 1978, 1979) with Platnick's (1981) reinterpretations, I hope I have underlined the importance of the new Flora Mesoamericana project as an empirical data base for future biogeographical studies on plants from this fascinating part of the Neotropics.

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THE ENIGMA OF THE CENTRAL AMERICAN HERPETOFAUNA: DISPERSALS OR VICARIANCE?[1]

JAY M. SAVAGE[2]

Some years ago, I essayed to elucidate the biogeographic history of the amphibians and reptiles of Central America, based upon the then available facts of distribution, understandings of phylogenetic relationships and climatic and geologic correlates (Savage, 1966). In subsequent biogeographic studies on the role of the region in the evolution of world frog faunas (Savage, 1973) and of neotropical mammals (Savage, 1974), I alluded to confirming and contradictory new evidence that affected my earlier interpretation.

The essential conclusions reached in 1966 were that: 1) the recent herpetofaunas of Central America are based upon a fundamental core of autochthonous groups whose history in the region goes back to Eocene-Oligocene times; 2) coexisting and evolving in association with the autochthonous groups throughout the region is a series of groups derived from northern sources; 3) the contribution of South American groups to the herpetofauna is minimal, except in extreme eastern Panama, and reflects Pliocene to Recent dispersal across the newly emergent Isthmian link between northwestern South America and lower Central America; 4) the autochthonous Central American groups had an ancient common ancestry with the South American stocks, but the two had undergone independent evolution in isolation in Central America and South America, respectively, during most of the Tertiary; and that 5) the relationship between the autochthonous and South American groups reflects a previous land connection between the two regions prior to Eocene times.

While no one has directly addressed these conclusions nor attempted to refute them, the studies of Savage (1974), Webb (1977, 1978), and Marshall et al. (1981) on mammals, Raven and Axelrod (1974) for angiosperms, and Bussing (1976) for freshwater fishes are not concordant with them. More importantly, recent interpretations of the geology of the Isthmian region (Malfait & Dinkelman, 1972; Marshall et al., 1979) raise doubts regarding the age of the pre-Eocene land connection between North and South America and place it so far back in time (100 m.y. B.P.) as to antedate seemingly the origin of most extant Central American groups. In addition, Rosen (1976, 1978) has developed a powerful explanatory

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[1] The present paper forms a continuation of the study of evolution and biogeography of the Central American biota carried out during my tenure as a John Simon Guggenheim Fellow (1963–1964). During the interval since the appearance of my 1966 papers, I have had continuous support for my activities in Central America from the Allan Hancock Foundation, the Organization for Tropical Studies (OTS), and the Universidad de Costa Rica. The kindness and cooperation of many individuals from these organizations is gratefully acknowledged.

I also wish to thank the graduate students in my biogeography course and several seminars in biogeography given at the University of Southern California (1975–1981) for critical comments and discussion on my ideas relating to Central American geology, geography, and biota, as presented in this paper. Finally, thanks go to Steven D. Werman of the University of Southern California for preparation of the figures.

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model of Central American biogeography based upon a number of major animal groups, which does not seem to support my ideas of 15 years ago. Duellman (1979), without directly acknowledging Rosen as his source, presented a brief explanation of the possible interchange of herpetofaunal components between North and South America, based upon Rosen's (1976) model.

For these reasons, and because our knowledge of distributions, fossil history, and phylogenetic relations for the amphibians and reptiles of Central America have substantially increased in the interim, the time seems ripe for a reconsideration of their biogeography. That the period since the appearance of my original paper has seen a major revolution in geological thinking associated with the theory of continental drift and the new tectonics (Uyeda, 1978) and the subsequent emergence of a new model for biogeographic explanation (Croizat et al., 1974; Nelson & Rosen, 1981), provides further stimulus for preparation of the present report.

It is not my purpose in the present study to reconstitute the entire data base nor recapitulate in detail the arguments and explanation of herpetofaunal history developed in my earlier paper (Savage, 1966). I have attempted to provide a revised summary of basic distributional data for Central America as part of this study. Otherwise, I have avoided repetition of materials and ideas presented in the 1966 report, particularly where there seems no reason to re-examine or modify major points or conclusions. This is especially the case with regard to characterization of subdivisions of the Mesoamerican herpetofauna, the recognition of relationship between post-Eocene events of physiographic and climate changes and concordant distribution patterns and the epigenetic influences (sensu Rosen, 1978) of Pleistocene-Recent climatic and vegetational fluctuations.

Composition and Distribution of the Herpetofauna

Although the focus of the present report is on Central America, as will be seen below, reference to adjacent tropical lands and physiographic subdivisions is necessary throughout. The following terminology is consistently employed for present land areas:

North America—the continental land mass lying west and north of the Isthmus of Tehuantepec

South America—the southern continental land mass extending east and south from eastern Panama

Central America—the region running southeast from the Isthmus of Tehuantepec to northwestern South America, including the Isthmus of Panama

Mesoamerica or Middle America—Mexico and Central America

Nuclear or upper Central America—the northern portion of Central America extending from the Isthmus of Tehuantepec to the uplands of northern Nicaragua; land positive throughout Cenozoic

Isthmian Link or lower Central America—the southern portion of Central America lying between southern Nicaragua and Colombia; submerged through much of Tertiary.

Wauchope and West (1964) and Stuart (1966) have outlined the major physiographic, hydrographic, climatologic, and vegetational aspects of the region. Duellman (1966, 1979), Savage (1966), and Rosen (1978) provide additional in-

formation as it relates to faunal distribution. Stuart (1966), Dengo (1968), Malfait and Dinkelman (1972), and Rosen (1976) provide much data on geologic features and their evolution.

The distributional data forming the basis for this account include the sources cited in my earlier work (Savage, 1966) and a host of more recent works, especially Duellman (1970, 1979), Henderson and Hoevers (1975), Lee (1980), Meyer and Wilson (1971, 1973), Villa (1972), Savage (1980a, 1980b), Wake and Lynch (1976), and the primary taxonomic literature cited in these reports.

The herpetofauna of Central America is comprised of nearly 700 species of amphibians and reptiles grouped by genera as follows: caecilians (4), salamanders (5), frogs and toads (33), turtles (9), lizards (40), snakes (76), and crocodilians (2), for a total of 42 amphibians and 127 reptiles (grand total 169). It forms the major portion of a somewhat more extensive tropical herpetofauna that ranges westward and northward from the Isthmus of Tehuantepec along the lowlands and premontane slopes of Mexico to about the level of Tamaulipas on the Atlantic and Sinaloa on the Pacific versant; in addition, it intermixes in a complex fashion with representatives of the northern or Nearctic herpetofauna in the mountains bordering the central plateau of Mexico on the east, west, and south. For purposes of this paper, the combined fauna of 197 genera, caecilians (4), salamanders (9), frogs and toads (37), turtles (9), lizards (45), snakes (91), and crocodilians (2), of the area is considered as a single unit, the Tropical Mesoamerican herpetofauna.

These genera may be placed into one of four major groupings based upon distribution: 1) widespread tropical—tropical genera found throughout the Middle and South American tropics with equally strong species differentiation in both regions; 2) South American—genera with centers of distribution and differentiation in South America; 3) Tropical Middle American—genera with centers of distribution and differentiation in tropical Mexico and Central America; and 4) Extratropical North American—genera with centers of distribution and differentiation in extratropical Mexico or the United States. A number of distinctive patterns of distribution within the four major groupings are evident and provide a basis for evaluating the composition of the Central American herpetofaunas as follows:

1. WIDESPREAD TROPICAL (11)

Eleutherodactylus
Bufo
Phrynohyas
Hyla
Mabuya
Leptotyphlops
Drymarchon
Drymobius
Spilotes
Micrurus
Bothrops

2. SOUTH AMERICAN (60)

A. Northern Limit of Range in Panama (22)

Caecilia
Oscaecilia
Enyalioides
Echinosaura

Protopipa
Rhamphophryne
Chiasmocleis
Elachistocleis
Relictivomer
Gastrotheca
Hemiphractus
Pleurodema
Chelonoides
Morunasaurus
Amphisbaena
Trachyboa
Atractus
Diaphorolepis
Lygophis
Phimophis
Pseudoboa
Siphlophis
Bothriopsis

B. Northern Limit of Range in Costa Rica (20)

Glossostoma
Phyllobates
Colostethus
Phyllomedusa
Atelopus
*Anolis**
Polychrus
Bachia
Leposoma
Ptychoglossus
Neusticurus
Anadia
Anomalepis
Helminthophis
Liotyphlops
Epicrates
Helicops
Leimadophis
Nothopsis
Tripanurgos

* *Anolis* reaches southern United States via the West Indies.

C. Northern Limit of Range Between Costa Rica and Guatemala (6)

Dendrobates
Corallus
Chironius
Erythrolamprus
Rhinobothryum
Lachesis

D. Northern Limit of Range in Mexico (11)

*Leptodactylus**
Physalaemus
Centrolenella
Ameiva
Gonatodes
Gymnophthalmus
Typhlops
Clelia
Oxyrhopus
Xenodon
Caiman

* Reaches southern United States.

3. TROPICAL MIDDLE AMERICAN (105)

A. Endemics (32)

Bolitoglossa B
Pseudoeurycea
Chiropterotriton B
Triprion
Plectrohyla
Ptychohyla
Anotheca
Coloptychon

Claudius
Staurotypus
Dermatemys
Corytophanes
*Aristelliger**
Laemanctus
Ctenosaura
Enyaliosaurus
Lepidophyma
*Celestus**
Xenosaurus
Crepidophryne
Loxocemus
Adelphicos
Amastridium
Crisantophis
Conophis
Hydromorphus
Leptodrymus
Scolecophis
Symphimus
Tantillita
Trimorphodon
Crocodylus

* Also in Antilles.

B. Northern Limit of Range in Extratropical North America (17)

Rhinophrynus
Hypopachus
Gastrophryne
Syrrhophus
Kinosternon
Coleonyx
Phyllodactylus
Heloderma
Cnemidophorus
Coniophanes
Ficimia
Oxybelis
Leptodeira
Rhadinaea
Tantilla
Trimorphodon
Crocodylus

C. Southern Limit of Range in Northern and/or Northwestern South America (21)

Dermophis
Gymnopis
Oedipina
Smilisca
Rhinoclemmys
Basiliscus
Lepidoblepharis
Thecadactylus
Ungaliophis
Coniophanes
Dendrophidion
Enulius
Geophis
Ninia
Pliocercus
Scaphiodontophis
Sibon
Stenorrhina
Tretanorhinus
Bothriechis
Crocodylus

D. Southern Limit of Range in Amazon Basin or Farther South (17)

Bolitoglossa A
Norops
Iguana
Sphaerodactylus
Phyllodactylus
Cnemidophorus
Dipsas
Imantodes
Leptodeira
Leptophis
Mastigodryas
Oxybelis

Pseustes
Diploglossus *Rhadinaea*
Boa *Tantilla*

E. Endemic Genera in Tropical Mexico (19)

Chiropterotriton A *Chersodromus*
Lineatriton *Cryophis*
Parvimolge *Geagras*
Thorius *Manolepis*
*Hylactophryne** *Pseudoficimia*
Tomodactylus *Rhadinophanes*
*Pternohyla** *Sympholis*
Anelytropsis *Tantalophis*
Bipes *Toluca*
Exiliboa

* Occurs in southern United States.

4. EXTRATROPICAL NORTH AMERICAN (33)

A. Southern Limit of Range in Tropical Mexico (15)

1) Southern Limit of Range in Central or Southern Mexico (9)

Phrynosoma *Rhinocheilus*
Urosaurus *Sonora*
Ophisaurus *Salvadora*
Gyalopion *Scaphiopus*
Hypsiglena

2) Southern Limit of Range Marginally Tropical (6)

Notophthalmus *Holbrookia*
Callisaurus *Arizona*
Dipsosaurus *Micruroides*

The latter six genera are not treated further in this report and have been included here only for the sake of completeness.

B. Southern Limit of Range in Central America (12)

Terrapene *Abronia*
Sceloporus *Gerrhonotus*
Eumeces *Nerodia*
Sphenomorphus *Elaphe*
Pituophis *Thamnophis*
Storeria *Agkistrodon*

C. Southern Limit of Range in South America (6)

Rana *Coluber*
Chelydra *Lampropeltis*
*Chrysemys** *Crotalus*

* Includes *Pseudemys*.

These data demonstrate that the recent Central American herpetofauna is composed primarily of genera with one of two major distribution patterns. One group includes genera with a tropical Middle American distribution pattern that predominate in Central America at all elevations from the Isthmus of Tehuantepec to central Panama and in the lowlands on both coasts of Mexico, to the limits of tropical conditions. The second group includes genera with a South American distribution pattern and is fully represented in the region only in Panama. Of the 197 genera in tropical Mesoamerica, 53% are centered essentially there, 30% are South American, and 17% are extratropical North American (Nearctic) in distribution. North of Costa Rica only 18 genera (9%) are South American groups, while in eastern Panama around 60% of the genera are South American. These data and the distribution of the 55 New World families of amphibians and reptiles (Table 1) support the idea developed in my 1966 paper that the tropical Mesoamerican herpetofauna is a distinctive assemblage only distantly related to that of South America and even less so to that of extratropical North America.

General faunal relationships between tropical Middle America and South America is suggested by family distributions. Only seven families found in Central America do not range into South America and only 10 are conversely found in South America but not in tropical Middle America. Nevertheless, the herpetofaunas of the two regions each stands as an unique combination of families, subfamilies, genera, and species groups. A comparison at the generic level will suffice to emphasize the degree of faunal difference. Of the 169 genera in the herpetofauna of Central America, 32 are endemic to the area and 21 others are essentially restricted to the region. Only 16 rather wide-ranging South American genera occur in Central America north of Costa Rica, while the South American continent supports about 200 endemic genera that are not known from north of Colombia. A sample of the Neotropical endemics is provided in the list below, with emphasis on tropical groups:

Gymnophiona: *Rhinatrema, Siphonops, Typhlonectes.*

Anura: *Pipa, Adenomera, Ceratophrys, Crossodactylus, Cycloramphus, Hylodes, Eupsophus, Odontophrynus, Pseudis, Pseudopaludicola, Thoropa, Zachaenus, Dendrophryniscus, Melanophryniscus, Brachycephalus, Amphignathodon, Aparasphenodon, Cryptobatrachus, Nototheca, Osteocephalus, Tetraprion, Ctenophryne, Dermatonotus, Elachistocleis, Synapturanus.*

Testudinata: *Podocnemis, Batrachemys, Chelys, Hydromedusa, Phrynops.*

Sauria: *Aptycholaemus, Hoplocercus, Liolaemus, Ophryoessoides, Plica, Stenocercus, Tropidurus, Urocentron, Coleodactylus, Homonota, Dicrodon, Dracaena, Euspondylus, Kentropyx, Proctoporus, Tupinambis, Leposternon.*

Serpentes: *Anilius, Eunectes, Apostolepis, Drepanoides, Drymoluber, Elapomorphus, Hydrops, Liophis, Lystrophis, Philodryas, Sibynomorphus, Thamnodynastes.*

Crocodilia: *Melanosuchus, Paleosuchus.*

The facts of distribution reinforce the concept of the Middle American tropical assemblage as a distinctive unit, more or less equivalent to the Nearctic and Neotropical units. It must be emphasized that the Mesoamerican herpetofauna is not transitional between the Nearctic and Neotropical assemblages as proposed by Darlington (1957) but is comprised primarily of endemic genera, species groups,

TABLE 1. Distribution of New World families of amphibians and reptiles.

I. Restricted to One Geographic Region		
Nearctic (9)	Tropical Mesoamerica (5)	South America (9)
		Rhinatrematidae
		Typhlonectidae
Cryptobranchidae		
Sirenidae		
Proteidae		
Amphiumidae		
Ambystomatidae		
Salamandridae		
Ascaphidae	Rhinophrynidae	Pipidae*
Pelobatidae		Rhinodermatidae
		Brachycephalidae
		Pseudidae
Trionychidae	Dermatemydidae	Pelomedusidae
	Dibamidae	
	Xenosauridae	Chelidae
	Loxocemidae	Aniliidae
II. Occurring in Two Regions		
Nearctic-Tropical Mesoamerica (2)	South America-Nearctic (1)	Tropical Mesoamerica-South America (6)
Xantusiidae	Testudinidae*	Caeciliidae
Helodermatidae		Dendrobatidae
		Centrolenidae
		Gymnophthalmidae
		Anomalepididae
		Typhlopidae
III. Occurring in All Three Regions (22)		
Plethodontidae	Iguanidae	Micruridae
Microhylidae	Gekkonidae	Viperidae
Leptodactylidae	Teiidae	Crocodylidae
Bufonidae	Scincidae	
Hylidae	Anguidae	
Ranidae	Amphisbaenidae	
Kinosternidae	Leptotyphlopidae	
Chelydridae	Boidae	
Emydidae	Trophidophiidae	
	Colubridae	

* Reaching Eastern Panama.

and species, with a small representation of Nearctic forms and a somewhat larger sampling of groups with Neotropical affinities.

Six major herpetofaunal assemblages may be recognized in the Central American area (Fig. 1 and Table 2):

1. **Eastern and Western Lowland Herpetofauna**—a wide-ranging fauna, the most diverse and richest in species composition of the Central American assemblages, found along the Atlantic lowlands from Tamaulipas, Mexico, to central Panama; with more or less isolated segments at moderate elevations along the Pacific slopes of Guatemala and in the Golfo Dulce region in the Pacific lowlands of southwestern Costa Rica and extreme western Panama.

2. **Western Lowland Herpetofauna**—a fauna associated with semiarid to sub-

humid climatic conditions, ranging along the Pacific lowlands from northern Sinaloa in Mexico, to the Golfo de Nicoya region and Meseta Central of Costa Rica; including the subhumid and semiarid assemblages of Atlantic drainage valleys in Chiapas, Mexico, and Guatemala and the uplands of Honduras and Nicaragua; characterized by a predominance of lizard and snake species and virtual absence of salamanders.

3. **Guatemalan Highland Herpetofauna**—an assemblage restricted to the cool moist habitats of the Chiapas and Guatemala highlands.

4. **Talamancan Herpetofauna**—a fauna with a well-developed amphibian complement, occurring in the humid environments of highland Costa Rica and western Panama.

5. **Panamanian Herpetofauna**—a fauna associated with disjunct subhumid lowland habitats from eastern Panama, along the Pacific versant, to the Chiriqui region of western Panama; showing closest affinities to the herpetofaunas of northern lowland Colombia and Venezuela that are associated with subhumid to arid conditions along the Caribbean lowlands.

6. **Chocoan Herpetofauna**—a South American fauna, extremely rich in species composition, found along the Pacific lowlands from northern Ecuador through Colombia and barely entering eastern Panama, where it is found in the Darien region along the Caribbean versant.

THE FOSSIL RECORD

The fossil record for amphibians and reptiles in Central America is meager with only one tortoise genus ? *Chelonoides* recorded from Oligocene to Miocene in Costa Rica and a few Pleistocene examples of modern genera. The general fossil record for recent Central and South American families is summarized (Table 3) and commented on below.

It should be noted that the following extant families were represented in America north of Mexico as well: Salamanders—Cryptobranchidae (Cretaceous), Proteidae (Cretaceous, Eocene), Sirenidae (Cretaceous, Eocene), Amphiumidae (Cretaceous, Paleocene), Salamandridae (Cretaceous), and Pelobatidae (Pliocene-R). Two extant lizard families—Agamidae (Eocene), Varanidae (Cretaceous-Oligocene)—are also represented, but do not occur in the Americas at present.

The ancient, but contemporary turtle family Trionychidae occurs in North America as far back as Cretaceous and in the Pliocene of South America.

ORIGINS AND HISTORY OF THE HERPETOFAUNA: A REVIEW OF THE PROBLEM

In my earlier paper (1966), I concluded from an analysis of the distributional data, geologic, climatological, and vegetational correlates and changes, together with an assessment of phylogenetic relationships, that three major and one minor historical source units had contributed to the Central American herpetofauna.

The most important unit (the Middle American Element) is comprised of genera that are primarily tropical Mesoamerican in distribution and have their closest allies either in the region or in South America, but are mostly endemic to Central

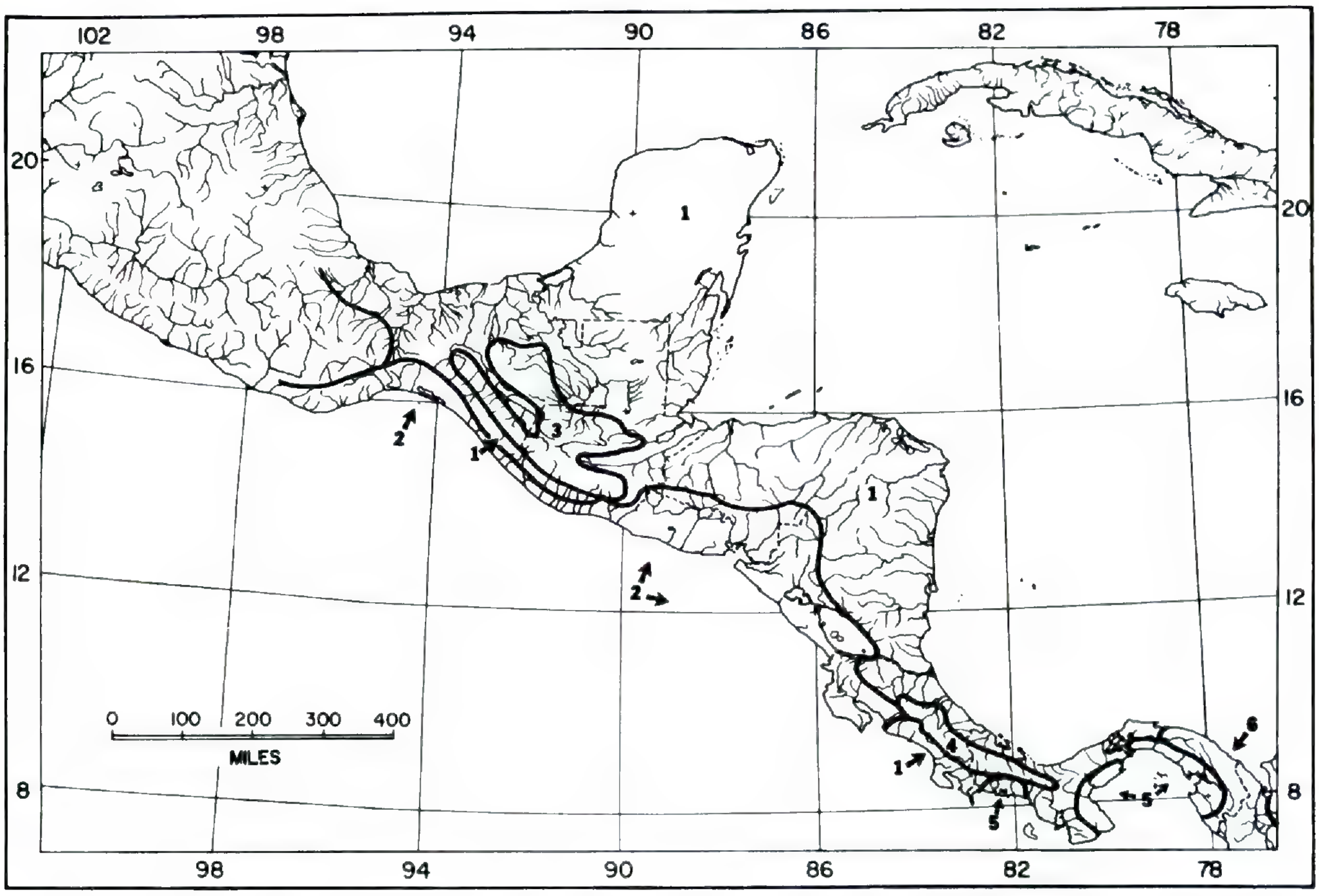


FIGURE 1. Major herpetofaunas of Central America. See text for description of assemblages denoted by numbers.

America and Mexico. Available evidence indicates that members of this unit and/or their ancestors had a more extensive range in North America in early Tertiary when humid warm climates occurred as far north as the region of what is now Montana, Wyoming, Utah, Colorado, and the Dakotas, but became restricted southward by climatic change in late Cenozoic to tropical Mesoamerica.

A second unit (the Old Northern Element) contains a series of genera that are primarily extratropical in distribution in Eurasia and/or North America, but are represented by several tropical forms in the Americas. These groups and/or their ancestors were distributed more or less continuously and circumpolarly in early Tertiary, but were forced southward and fragmented into distinct geographic isolates by the results of increased cooling and acidity through Cenozoic. Included in this stock is a unique Mesoamerican component of endemic families and genera that has evolved with the autochthonous Middle American unit from Eocene onward.

The third major group (the South American Element) is principally South American in distribution and relationships but occurs to various distances onto the Isthmian Link and northward. This stock obviously underwent evolution on the South American land-mass during most of Cenozoic and must be interpreted as a recent contributor to Central American faunal diversity.

The fourth minor unit (the Young Northern Element) in terms of the region under study is represented by a few genera that are primarily extratropical in distribution and associated with the semiarid to arid regions of the southwestern

TABLE 2. Distribution of Central American genera of amphibians and reptiles.

	Mesoamerican				South American	
	Humid E and W Lowland	Western Lowland	Guate-malan Highland	Tala-mancan Highland	Pana-manian	Chocoan
GYMNOPHIONA (4)						
Caecilia	X					X
Oscaecilia					X	X
Gymnopis	X					
Dermophis	X	X				X
CAUDATA (5)						
Bolitoglossa A	X		X	X		X
Bolitoglossa B			X	X		
Pseudoeurycea			X			
Chiropterotriton B			X	X		
Oedipina	X	X	X	X		X
ANURA (33)						
Protopipa					X	
Rhinophrynus	X	X				
Leptodactylus	X	X			X	X
Pleurodema					X	
Physalaemus	X	X			X	
Eleutherodactylus	X	X	X	X		X
Syrrhophus	X	X				
Dendrobates	X					X
Phyllobates	X					X
Colostethus	X					X
Centrolenella	X			X		X
Bufo	X	X	X	X	X	X
Crepidophryne				X		
Rhamphophryne						X
Atelopus				X		X
Smilisca	X	X		X	X	X
Phrynohyas	X	X			X	
Hyla	X	X	X	X	X	X
Plectrohyla			X			
Ptychohyla			X			
Hemiphractus	X					X
Gastrotheca	X					X
Anotheca	X					
Triprion	X					
Agalychnis	X					X
Phyllomedusa	X					X
Chiasmocleis					X	
Elachistocleis					X	
Relictivomer					X	
Glossostoma				X		
Gastrophryne	X	X				
Hypopachus	X	X	X			
Rana	X	X	X	X		X
TESTUDINATA (9)						
Kinosternon	X	X			X	X
Chelydra	X	X				X
Claudius	X					
Staurotypus	X	X				
Dermatemys	X					
Terrapene	X					

TABLE 2. Continued.

	Mesoamerican				South American	
	Humid E and W Lowland	Western Lowland	Guatemalan Highland	Talamancan Highland	Panamanian	Chocoan
Chrysemys	X	X			X	X
Rhinoclemmys	X	X				X
Chelonoides					X	
SAURIA (40)						
Anolis					X	X
Norops	X	X	X	X		
Polychrus	X					X
Basiliscus	X	X		X	X	X
Corytophanes	X					X
Laemanctus	X					
Morunasaurus	X					
Enyalioides						X
Sceloporus	X	X	X	X		
Ctenosaura	X	X			X	
Enyaliosaurus	X	X				
Iguana	X	X			X	X
Coleonyx	X	X				
Sphaerodactylus	X	X				
Lepidoblepharis	X					X
Gonatodes	X	X			X	X
Aristelliger	X					
Thecadactylus	X					X
Phyllodactylus	X	X				
Lepidophyma	X	X				
Eumeces	X	X				
Sphenomorphus	X		X			
Mabuya	X	X			X	X
Ameiva	X	X			X	X
Cnemidophorus	X	X			X	
Bachia	X				X	
Gymnophthalmus		X	X		X	
Leposoma	X					X
Echinosaura	X					X
Ptychoglossus	X					X
Neusticurus	X					
Anadia	X					X
Amphisbaena						X
Abronia			X			
Gerrhonotus			X	X		
Coloptychon	X			X		
Celestus	X			X		
Diploglossus	X					X
Xenosaurus			X			
Heloderma		X				
SERPENTES (76)						
Helminthophis				X		
Liotyphlops	X				X	X
Anomalepis	X					
Typhlops	X			X		
Leptotyphlops	X	X			X	
Boa	X	X			X	X
Corallus	X				X	X
Epicrates	X	X			X	

TABLE 2. Continued.

	Mesoamerican				South American	
	Humid E and W Lowland	Western Lowland	Guatemalan Highland	Talamancan Highland	Panamanian	Chocoan
Loxocemus		X				
Trachyboa						X
Ungaliophis	X	X				
Adelphicos	X		X			
Amastridium	X			X		
Atractus						X
Chironius	X	X			X	X
Clelia	X	X		X	X	X
Coluber	X	X			X	
Coniophanes	X	X				X
Conophis	X	X				
Crisantophis		X				
Dendrophidion	X				X	X
Diaphorolepis						X
Dipsas	X	X			X	X
Drymarchon	X	X			X	X
Drymobius	X	X			X	X
Elaphe	X	X				
Enulius	X	X			X	X
Erythrolamprus	X	X			X	X
Ficimia	X	X				
Geophis	X		X	X		
Helicops				X		
Hydromorphus	X			X		
Imantodes	X	X			X	X
Lampropeltis	X	X		X	X	X
Leimadophis	X			X	X	X
Leptodeira	X	X			X	X
Leptodrymus		X				
Leptophis	X	X			X	X
Lygophis	X					X
Mastigodryas	X				X	X
Nerodia	X					
Ninia	X	X	X	X	X	X
Nothopsis	X					X
Oxybelis	X	X			X	X
Oxyrhopus	X				X	X
Phimophis					X	
Pituophis			X			
Pliocercus	X					X
Pseudoboa					X	
Pseustes	X	X			X	X
Rhadinaea	X		X	X		X
Rhinobothryum	X					X
Scaphiodontophis	X	X			X	
Scolecophis		X				
Sibon	X	X				X
Siphlophis					X	X
Spilotes	X	X			X	X
Stenorrhina	X	X				X
Storeria	X					
Symphimus	X	X				
Tantilla	X	X		X		X
Tantillita	X					

TABLE 2. Continued.

	Mesoamerican				South American	
	Humid E and W Lowland	Western Lowland	Guatemalan Highland	Talamancan Highland	Panamanian	Chocoan
Thamnophis	X	X	X			
Tretanorhinus	X	X			X	X
Trimetopon	X	X		X		
Trimorphodon		X				
Tropidodipsas	X	X	X			
Tripanurgos	X					X
Xenodon	X	X			X	X
Micrurus	X	X			X	X
Agkistrodon	X	X				
Bothriechis	X	X	X	X	X	X
Bothriopsis						X
Bothrops	X	X	X	X	X	X
Lachesis	X					X
Crotalus	X	X				
CROCODILIA (2)						
Caiman	X	X			X	X
Crocodylus	X	X			X	X
Totals (169)	130	82	28	34	61	87

United States and adjacent Mexico. This unit contains many distinctive genera outside of Central America to form a significant component of the North American herpetofauna (Savage, 1960, 1966) and seems to have evolved *in situ* in response to increasing acidity and cooling trends in the latter portion of the Cenozoic.

It appeared that in early Cenozoic, the Americas (Fig. 2) were dominated by two major herpetofaunal units. In subtropical and tropical America, to at least 40°N latitude, a generalized tropical herpetofauna occurred. To the north were representatives of ancestral Old Northern groups. It was proposed, based upon correlation with geologic data (Vinson & Brineman, 1963), that the continuity of the generalized tropical herpetofauna was interrupted by the inundation of the Isthmian Link in late Paleocene. With the establishment of the open marine portal across the region from Nicaragua to Colombia, the two fragments of the generalized tropical unit underwent independent evolution to the north and south of the portal during most of the rest of the Tertiary. The distinctive Middle American and South American Elements were believed to have been the result of this fragmentation.

Apparently, certain representatives of the Old Northern Element (the Central American component) reached Middle America in Eocene and evolved in association with the Middle American Element for the remainder of Cenozoic. Subsequently, the events of mountain building and the drying and cooling trends that were initiated in Oligocene led to a southward latitudinal depression of tropical and subtropical conditions and with the resultant compression of the descendant species of the two stocks into the Middle American Peninsula. By the middle of

TABLE 3. Fossil records for extant families of the Central (X) and South American (*) herpetofaunas.

	Recent	Pleistocene	Pliocene	Miocene	Oligocene	Eocene	Paleocene	Cretaceous
Rhinatrematidae	*							
Caeciliidae	*						*	
Typhlonectidae	*							
Plethodonidae	*							
	X	X	X	X				
Pipidae	*						*	*
Rhinophrynidae	X				X	X		
Microhylidae	*							
	X	X		X				
Leptodactylidae	*	*	*	*	*	*	*	
Bufonidae	*	*	*	*				
	X	X	X					
Rhinodermatidae	*							
Brachycephalidae	*							
Dendrobatidae	*							
Pseudidae	*							
Centrolenidae	*							
Hylidae	*							
	X	X	X	X				
Ranidae	X	X	X					
Pelomedusidae	*	*	*	*		*	*	*
				X				X
Chelidae	*	*	*	*	*	*		
Kinosternidae	*							
	X	X	X					
Dermatemydidae	X					X	X	X
Chelydridae	X	X		X	X			
Emydidae	*	*						
	X	X	X	X	X	X	X	X
Testudinidae	*	*	*	*	*	*		
	X	X	X	X	X			
Iguanidae	*			*			*	*
	X	X	X	X	X	X		
Teiidae	*	*	*	*			*	
	X	X	X					X
Gekkonidae	*							
	X							
Scincidae	*							
	X	X	X	X	X	X	X	X
Gymnophthalmidae	*							
Dibamidae	X							
Xantusiidae	X	X				X	X	
Xenosauridae	X				X	X	X	X
Anguidae	*							
	X			X	X	X		
Helodermatidae	X				X			
Amphisbaenidae	*	*						
	X				X	X		
Anomalepididae	*							
	X							
Typhlopidae	*							
	X							
Leptotyphlopidae	*							
	X							

TABLE 3. Continued.

	Recent	Pleisto-cene	Pliocene	Miocene	Oligo-cene	Eocene	Paleo-cene	Creta-ceous
Loxocemidae	X							
Aniliidae	*			*				
				X			X	X
Boidae	*	*	*	*		*	*	
	X			X	X	X	X	
Tropidophiidae	X							
Colubridae	*	*		*				
	X	X	X	X				
Micruridae	*							
	X	X	X					
Viperidae	*	*						
	X	X	X					
Crocodylidae								
Crocodylinae	*	*	*	*	*	*	*	
Alligatorinae	*	*	*	*	*	*	*	

Oligocene, the tropical Mesoamerican region was isolated on the north by a temperate semiarid to arid climatic barrier that increased in extent throughout the remainder of the Cenozoic. The two isolating factors of the marine portal to the south and the climatic barrier to the north allowed for the *in situ* development of much of the typical tropical Mesoamerican herpetofauna during most of the Cenozoic.

When the Panamanian Isthmus was reformed in Pliocene, some South American groups dispersed into lower Central America and some Middle American and associated Central American stocks into South America. Nevertheless, tropical Mesoamerica, except in eastern Panama, is dominated by the autochthonous Middle American Element that indicates the long and independent *in situ* evolution of the herpetofauna. A summary diagram (Fig. 2) illustrates the principal features of this explanation.

Although there can be little argument regarding the distinctive nature of the core tropical Mesoamerican herpetofauna or that its major element has an ancient relationship to South American stocks, new geologic and biotic evidence and its interpretation raise into question my earlier explanation of how the observed patterns developed. The new evidence and its impact are discussed below in terms of geologic history, distributional data for other groups, and theoretical considerations.

A central feature of my attempt to explain the distinctiveness of the core Mesoamerican herpetofauna relates to the history of intercontinental land connections between Central and South America. Most recent geologic studies concur with the view of Dietz and Holden (1970), Malfait and Dinkelman (1972), and Ladd (1976), that there was no direct land connection between North America plus Nuclear Central America and South America, throughout most or all of Cretaceous and Cenozoic. Only with the establishment of the Isthmian Link, at

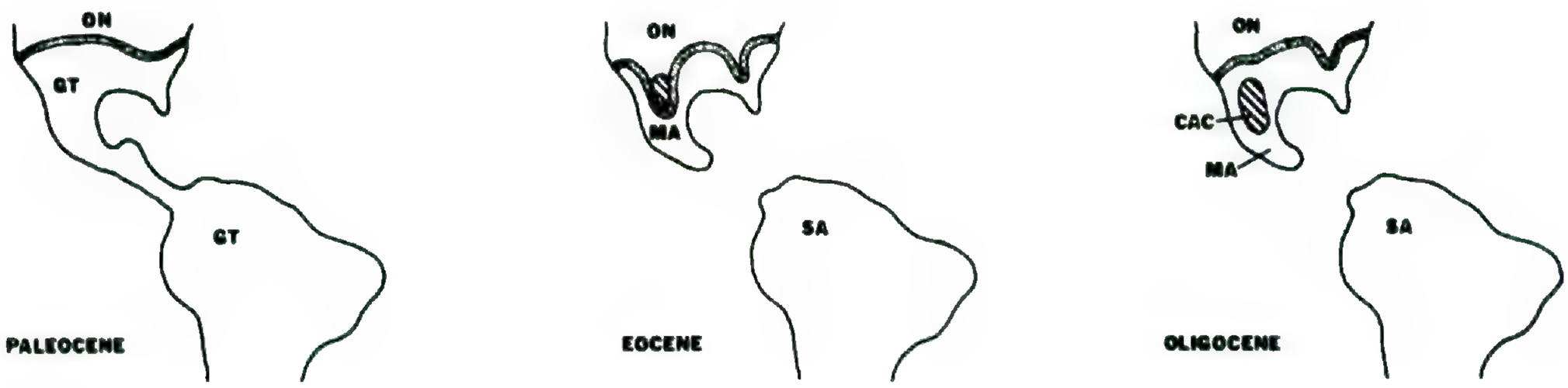


FIGURE 2. Origins and history of the Mesoamerican herpetofauna according to model of Savage (1966). See text for description of history of Old Northern (ON), Generalized Tropical (GT), Middle American (MA), South American (SA), and Central American Components (CAC).

the beginning of the Pliocene (Raven & Axelrod, 1974; Savage, 1974), about 5.2 m.y. B.P. or late Pliocene (3 m.y. B.P.) according to others (Simpson, 1950, 1969; Patterson & Pascual, 1968; Webb, 1977, 1978; Marshall et al., 1979) was there an opportunity for overland immigration between Central and South America. While there is a suggestion of a mid-Cretaceous connection of Nuclear Central America and South America (Smith & Briden, 1977), available data indicate a minimum period of separation between the two regions for about 100,000 m.y. During about half of that time interval, South America was an isolated island continent because direct land connections to Africa were eliminated by late Jurassic (140 m.y. B.P.) and with Antarctica-Australia by Eocene or Oligocene (50 m.y. B.P.).

A number of workers have suggested that a series of island arcs developed in the general area between Nuclear Central America and South America during late Cretaceous and early to late Tertiary. Dengo (1968, 1973) proposed that a volcanic chain extended across the portal region, somewhat south of the present isthmus from Cretaceous to Eocene. A second volcanic arc, the precursor of the present isthmus, appeared by the Oligocene at the level of present-day Costa Rica and Panama. Rosen (1976), on the basis of his interpretation of the work of Holden and Dietz (1972), and Malfait and Dinkelman (1972), hypothesized the presence of a late Cretaceous-Pliocene island arc (the proto-Antilles) in the portal region, that later became displaced far to the east by tectonic events associated with movements of the Caribbean plate.

Another group of workers (Owen, 1976; Carey, 1976; Shields, 1979), advocates of the expanding earth hypothesis, indicated that a land bridge or a series of closely proximate islands connected the region of present day Venezuela, the

Greater Antilles, the Nicaragua Plateau, and Nuclear Central America in late Cretaceous-Paleocene, with a possible connection between Cuba and Florida, as well. Carey (1976) further regarded the Panamanian Portal to have been open but only transitorily in Cenozoic and stated (p. 393), "and at no time from the Paleozoic to the present has there been any substantial marine barrier separating North and South America."

Lillegraven et al. (1979) developed a somewhat similar idea of an eastern archipelago in addition to those described by Dengo (1968, 1973) in the Panamanian Portal zone, perhaps influenced by the views of Carey (1976) and Shields (1979). The proposed archipelago probably persisted from late Cretaceous to Eocene and was formed by volcanic islands of the Aves Arc, which originally were located about 200 km further west than their submerged present day remnant, and the volcanic islands that were the predecessors of the Greater Antilles. The latter series terminated in close proximity to the now submerged Nicaragua Plateau, which was probably land positive and connected to Nuclear Central America (Perfit & Heezen, 1978).

These conflicting ideas and recent geologic studies on sea-floor and tectonic features in the region (Bowin, 1976; Christofferson, 1976; Hey et al., 1977; Londsdale & Klitgord, 1978) confirm the complexity of its history and the likelihood of the substantial uncertainties in interpretation for sometime to come. Nevertheless, the majority opinion rejects the notion of a continuous land connection between Central and South America for all of Cretaceous to Pliocene time. Therefore, the hypothesis of 1) a Paleocene land connection that existed in the region of the present Isthmian Link and permitted the wide distribution of a generalized tropical herpetofauna and 2) the fragmentation of that herpetofauna into Middle American and South American Elements by submergence of the land bridge, is brought into serious doubt. If, indeed, the tropical Mesoamerican and South American herpetofaunas are as distinctive as I claimed them to be in 1966, some other progenetic model for their differentiation needs to be found

Biogeography is based upon the recognition of concordant distribution patterns and attempts to explain their congruence. If the patterns I recognized for herpetofaunal distributions in 1966 have general significance, they should show concordance with the distributions of other organisms. In addition, the common patterns should provide clues to the cause of the observed congruence. Several major studies on the biogeography of Central America have appeared in the 15 years since my theory was published, especially Raven and Axelrod (1974) for seed-plants; Savage (1974), Webb (1977, 1978), Ferrusquia-Villafranca (1978), and Marshall et al. (1979) for mammals; Bussing (1976) for freshwater fishes; and Duellman (1979) for the South American herpetofauna. In the following paragraphs, the degree to which this paper recognizes patterns that are concordant or discordant with herpetofaunal ones is briefly explored.

Raven and Axelrod (1974) compared the situation among angiosperms in Central America to that in Australasia. In the latter region, the typical tropical Asian vertebrate fauna occurs eastward along the Indo-Malayan island chain to near the region of Wallace's Line (Darlington, 1957). East of this area through New Guinea, Australia, and associated islands, a markedly different fauna is present. Unlike the vertebrates, the flora is essentially similar from southern Asia, through

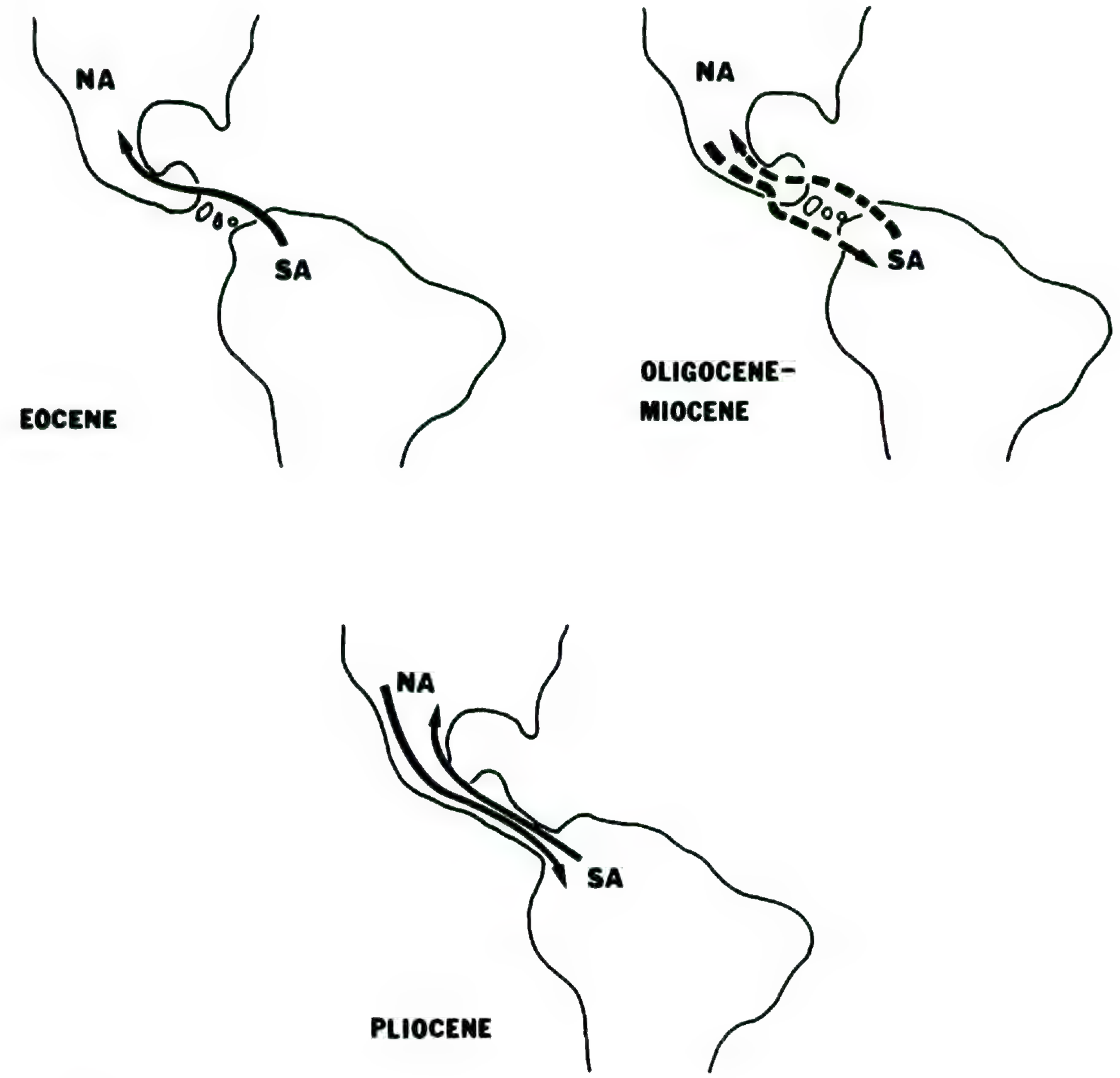


FIGURE 3. Origins and history of the Mesoamerican angiosperm flora, according to the model of Raven and Axelrod (1974). See text for description of history of North (NA) and South American (SA) derivatives.

New Guinea, northern Australia, and eastward to Fiji. According to Raven and Axelrod, the Central American vertebrate fauna has retained a level of distinctiveness. They argue that these differences have to do with the better powers of plants for overwater and waif dispersal. They suggest that until the Isthmian Link was established, the faunas on either side were distinctive and well-differentiated (as if on either side of Wallace's Line), while the flora north of the marine portal was not, and corresponded to the flora east of Wallace's Line. The subsequent blurring of the differences between faunas by overland immigration in both directions across the link has led to the current resemblances among the biotas throughout tropical America.

In essence, Raven and Axelrod proposed that Central America was populated by many plant families from South America through overwater and/or island-hopping dispersal in Eocene-Oligocene times. These groups joined a substantial suite of North American families. Subsequently, dispersals in both directions,

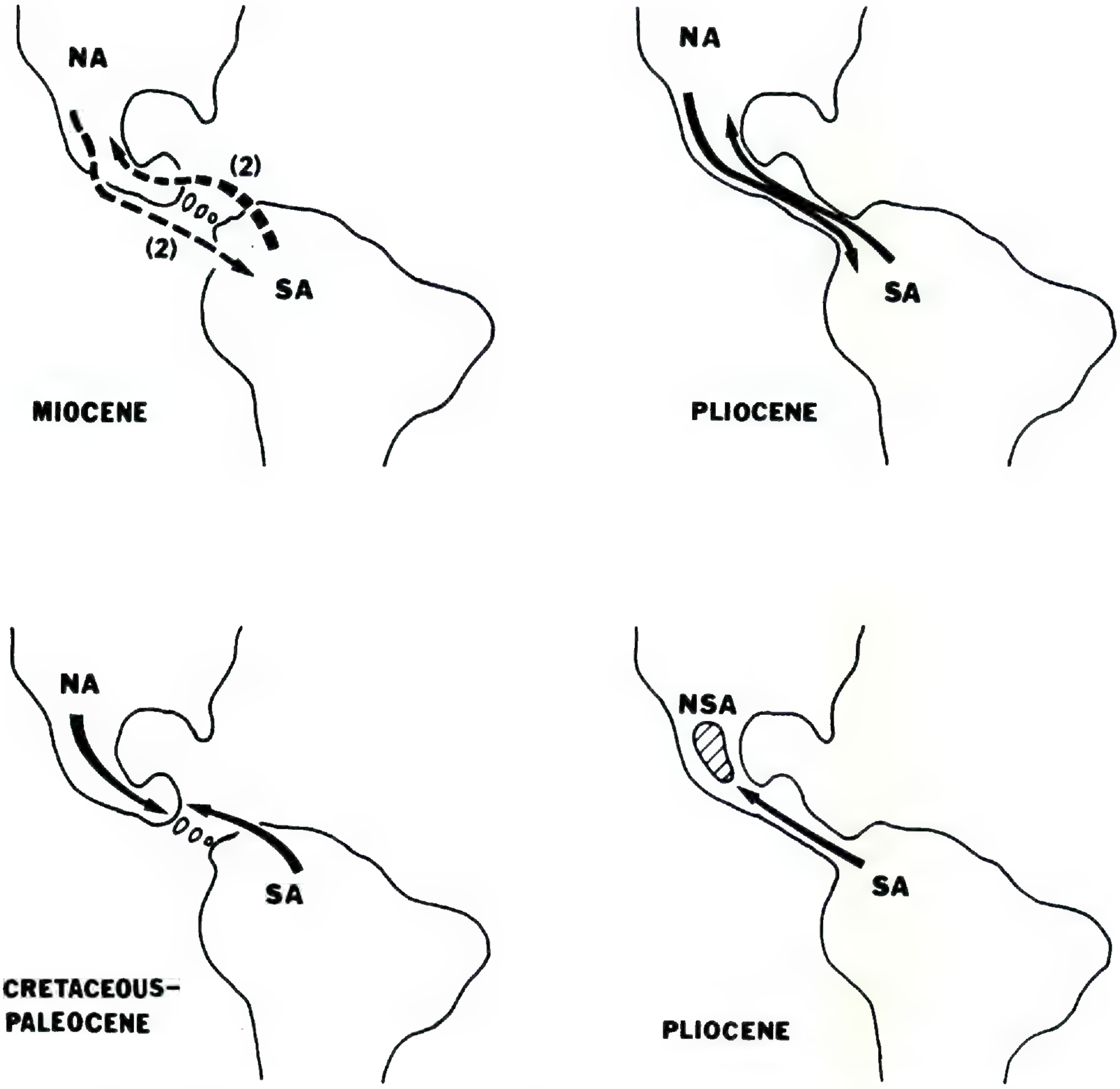


FIGURE 4. Origins and history of the Mesoamerican mammal fauna (upper) and freshwater fish fauna (lower), according to Marshall et al. (1979) and Bussing (1976), respectively. See text for explanation of history of North (NA) and South American (SA) and endemic Middle American (NSA) components.

first across the Central American archipelago and later across the emergent land connection, added to the floras of both Central and South America. These ideas on plant dispersal patterns are presented in a summary figure (Fig. 3).

Savage (1974), Webb (1977, 1978), Ferrusquia-Villafranca (1978), and Marshall et al. (1979) have reviewed the history of the relationships of Central and South American mammal faunas. These studies up-date the earlier treatments of Simpson (1950, 1969), Hershkovitz (1966, 1969), and Patterson and Pascual (1968). While differing, to some degree, the first group of authors agree that the Central and South American regions were essentially isolated from one another by the Panamanian Portal for most of Cretaceous and Tertiary. Minor dispersals from the south to the north (two families of ground sloths) and north to south (a genus to raccoon and the ancestor of a series of endemic cricetid mouse genera) occurred in Miocene. An extensive and balanced exchange took place over the

Isthmian Link in Pliocene-Recent times. The idea that the ancestors of caviomorph rodents and South American primates arrived by overwater dispersal from North America earlier in the Tertiary is not now generally accepted. In consequence, the mammal fauna of tropical Middle America was almost exclusively northern in its relationships until the Isthmian Link appeared and allowed a mixing with southern elements (Fig. 4).

Bussing (1976) reviewed the freshwater fish data for the region, with emphasis on island-hopping dispersal of South American groups in late Mesozoic and/or early Tertiary times. These groups underwent development *in situ* until the emergence of the Isthmian Link. Some groups of northern relations were also in the region. Subsequent to the establishment of the land connection to South America, additional southern stocks invaded Central America, but the endemic Central American lines did not re-invade South America (Fig. 4).

Duellman (1979), in the introductory chapter of a major symposium on the biogeography of the South American herpetofauna, briefly reviewed the problem of Central American relationships. While accepting the overall validity of my 1966 study, he recognized the difficulty presented by the geologic evidence for no land connection between the two areas over most of Cretaceous and Tertiary. As a result, he followed Bussing's (1976) and Rosen's (1976, paper to be discussed below) ideas of a dispersal route across the early proto-Antilles (late Cretaceous-Paleocene) and later Central American archipelago as a modus for producing major aspects of present patterns. Duellman's explanation requires a minimum of 17 dispersals at the family unit level (family or subfamily or tribe) in this fashion. He, of course, regards the emergent Isthmian Link as a dispersal route in both directions for previously isolated components in Central and South America, while confirming my conclusion that the influence of the southern immigrants on the herpetofauna of Middle America is minimal north of Panama.

These biological data sets, as interpreted above, are somewhat at variance with my 1966 conclusions, based upon herpetofaunal evidence. First, all of the mentioned authors favor overwater, island-hopping and/or waif dispersal as providing the principal source of extensive (plants, amphibians, and reptiles), moderate (freshwater fishes), or slight (mammals) South American group contributions to Central America prior to the final emergence of the Isthmian Link. Second, no distinctive Middle American component is recognizable for mammals. Third, Raven and Axelrod (1974) believed that angiosperms agree with the mammal pattern in lacking a recognizable Middle American component, except that they believed that dispersal from South America occurred over much of Cenozoic, while most South American mammals reached the area only in Pliocene to Holocene times.

In contrast, the data for freshwater fishes (Bussing, 1976) are more congruent with herpetofaunal patterns than are those for mammals and plants. Bussing recognized the distinctiveness of a Middle American component of the ichthyofauna, which is of South American origin, but which underwent evolution in isolation from the latter during much of Tertiary. Duellman (1979) concurred with my recognition of allied, but distinctive Middle and South American Elements in the herpetofauna.

The apparent non-congruence of the several sets of distributional data, if the data are accepted at face value, suggests that a) the history of plants and mammals in the region was substantially different than for fishes, amphibians, and reptiles, b) that some major differences in mode of interpretation of the data exist among students of the different groups, or c) that some mixture of these two alternates is involved. These latter two points lead directly to a consideration of theoretical issues which contribute to the problem in biogeographic interpretation as it applies to Central America.

During the last decade, a resurgence of interest in biogeographic theory has been engendered by the wide acceptance of continental drift and a new approach to attacking biogeographic problems (Nelson & Rosen, 1981). Prior to 1970, almost all biogeographic studies accepted the overall position of continental and ocean basin stability and dispersal as the major guide-posts for theory construction. In the 1970s, a new school of biogeographers, led by Gareth Nelson (1973, 1975) in association with his colleagues, Donn Rosen and Norman Platnick, invented vicariance biogeography. Although paying homage to Leon Croizat as the group's founder (Croizat, Nelson & Rosen, 1974) and later discovering an intellectual precursor in de Candolle (Nelson, 1978; Nelson & Platnick, 1981), the framework of ideas and the vigor and relative rigor of biogeographic hypothesis-testing developed by this group is original with them. They characterized the approach of earlier workers (Darwin, 1859; Wallace, 1876; but especially Matthew, 1915; Simpson in many papers republished as a book in 1965) as dispersal biogeography. Since the presumed differences between the two views, enumerated as a bill of particulars by the vicariance school (Croizat, Nelson & Rosen, 1974; Platnick & Nelson, 1978; Nelson & Platnick, 1981) against their rivals, are significant, they will be discussed in more detail in a later section. At this point, however, consideration must be given to the vicariance model of Central American biogeography developed by Rosen (1976, 1978) as it affects the problem of herpetofaunal history.

Rosen's (1976) study was aimed at a broad goal, the interpretation of the terrestrial, freshwater, and marine biogeography of the Caribbean region from the viewpoint of vicariance theory. In fact, his paper is the only precise exposition of the vicariance biogeographic method for a substantial geographic region. Because both the methodology and conclusions were innovative, the study is already considered a classic despite recent evidence (Patterson, 1981; Pregill, 1981) that the geological interpretations need revision. Although Rosen's theory of Caribbean biogeography also dealt with the history of marine groups and the Antilles, the following discussion is directed primarily to his ideas as they relate to the Central American biota. The essence of his vicariance model is summarized below:

1) a late Cretaceous proto-Antillean archipelago, lying in the region of the Panamanian portal, allowed for dispersal of South American groups into Nuclear Central America and for North American stocks into the archipelago (dispersal)

2) the movement of the proto-Antilles eastward created the Panamanian portal

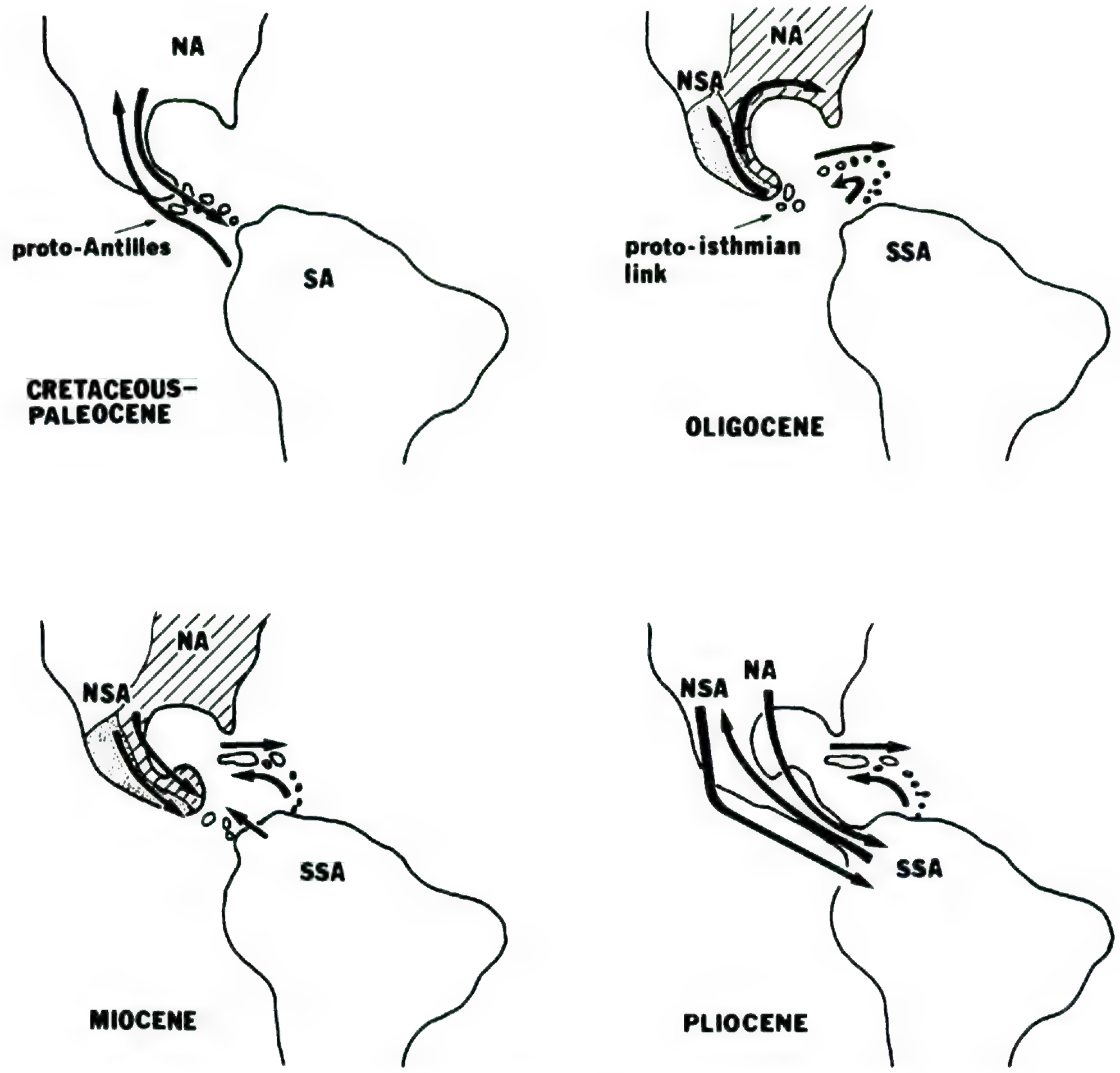


FIGURE 5. A vicariance model of Caribbean biogeography, according to Rosen (1976). See text for explanation; NA = North American, SA = South American, SSA = Southern South American, NSA = Central American stocks.

of early Tertiary that isolated North America from South America and allowed North American (NA) and South American derivatives (NSA) in Central America to evolve in isolation from stocks (SSA) in the southern island continent (vicariance)

3) the emergence of the Panamanian Isthmus in late Tertiary created a route for dispersal of South American groups (SSA) into Central America and Central American groups (NA + NSA) into South America (dispersal).

Two points are to be emphasized from this summary. First, Rosen indicated that South American groups reached Central America over the proto-Antilles archipelago, but contrary to Patterson's (1981) interpretation, North American groups dispersed no further than the archipelago. Second, Rosen recognized the distinctive nature of the Middle American fauna (isopods, onychophorans, spiders, butterflies, frogs and toads, lizards, snakes, birds, bats, monkeys, hystricomorph rodents, and particularly freshwater fishes), but included it as part of

his South American-Caribbean unit (track) to emphasize the presumed ancient continuity of distribution (Fig. 5).

The above review indicates the several areas of discordance with my 1966 model for herpetofaunal history in Central America. One is the conflicting geological evidence that centers on a consensus that there was no land connection between Central and South America for most of Cretaceous and Tertiary. Second is the apparently conflicting data from the distribution of other groups (plants, mammals, and freshwater fishes). Finally, the use of the newly developed theory and methodology of vicariance biogeography as applied to a wide variety of organisms in the development of a model of Caribbean biogeography, apparently, does not produce results congruent with my 1966 report.

For these reasons, it seems appropriate to re-evaluate the distributional data, the apparent patterns of distributional congruence, the interpretation of the patterns, and the model I developed in 1966 to explain the origins and history of the herpetofauna of the region. This resynthesis will include a consideration of the central theoretical problem of biogeography (dispersal versus vicariance); a reanalysis of the data of distribution using a different methodology in order to determine historical source units; development of a biogeographic model for the Central American herpetofauna; and comparison of the model to the distributional data for other groups and with geologic events.

The Central Theoretical Problem: Dispersal Versus Vicariance

The raw data of historical biogeography are the distributions (or tracks) of individual species in space (geographical ecology) and time. Because each species has its own set of peculiar ecological requirements and its own unique evolutionary history, each species has a discrete non-random ecogeographic distribution. As a consequence, no species is universally present and many species have very small or unique tracks.

The first level of generalization in biogeography is based on the recognition that in spite of the unique nature of individual species distributions, many individual tracks are concordant to show a common pattern. Determination of the patterns (generalized tracks) involving the coincident distribution of many species or several monophyletic groups (genera, families, etc.) of species is the fundamental first step in biogeographic analysis.

The second level of generalization in this process is to recognize the several disjunct adjoining or distant clusters of distributions that form nodes or track components within the generalized track. These components may be regarded as defining the geographic limits of major modern biotas, characterized by a high degree of endemism.

A third level of generalization attempts to tentatively identify the historical source units (ancestral biotas) that contributed to the modern biotas. In any given region, the biota may have been derived from several historical source units at different times, but usually the dominant source unit has developed *in situ* and is a component of a major generalized track.

In the remainder of this section, I will discuss the essential conceptual features of the two major current competing theoretical constructs that attempt to interpret

the recurrent coincident distribution patterns (generalized and component tracks) to produce explanations of biogeographic history.

As mentioned above, the field of historical biogeography has undergone a major revitalization during the last decade through the development of an original approach to biogeographic thinking, the vicariance theory, which seems to fit very well with the facts of continental drift and the new tectonics. The chief architects and proponents of vicariance (Croizat et al., 1974; Rosen, 1974: 321, 1976, 1978; Nelson & Rosen, 1981; Nelson & Platnick, 1981) maintain that their approach is superior to all others as a general explanation of pattern, primarily because it is more rigorously analytical and establishes historical hypotheses that may be independently tested by phylogenetic and/or geologic evidence. Ball (1976), McDowell (1978), and Pielou (1981), and to a lesser extent, Patterson (1981), have effectively countered this claim, without seriously weakening the fundamental strengths of vicariance biogeographic analysis, especially as it has evolved in its latest phases (Rosen, 1978; Platnick & Nelson, 1978; Morse & White, 1979), through association with cladistic studies of phylogenetic relationships.

The adherents of vicariance theory (vicariists *à la* Pielou, 1981) lump, willy-nilly, a host of alternate biogeographic explanations, methods, and analyses of distribution under the rubric of dispersal biogeography as an alternative, but essentially unscientific approach with which they take issue on every ground (Croizat et al., 1974; Platnick & Nelson, 1981). Unfortunately, to date, the only formulation of dispersal theory, in this context, has been by the vicariists, who have attributed all kinds of errors of procedure, philosophy, fact, and concept to the opposition. In this sense, dispersal biogeography is not a coherent set of concepts, but is a straw-man set up by vicariists, to emphasize the strengths of their own approach against a diffuse set of ideas attributed to dispersalists. Viewpoints as diverse and contradictory as: northern origin of groups and southward dispersal over stable continents (Matthew, 1915, and Simpson, 1965); Asian tropical origin of groups and radiation over stable continents to elsewhere (Darlington, 1957); dispersals by drifting continents (Raven & Axelrod, 1974; Savage, 1974); so-called island biogeography (MacArthur & Wilson, 1967); dynamic biogeography (Udvardy, 1969); and "phylogenetic" (= cladistic) biogeography, combining dispersal and vicariance (Hennig, 1966; Brundin, 1972, 1981) among others are placed within the dispersalist orb by vicariists.

Superficially, the dichotomy in biogeographic thought between dispersalists and vicariists seems to be one of emphasis. The former emphasize the active or passive dispersion of organisms as the principal agent responsible for patterns. The latter regard dispersal as relatively unimportant in producing present patterns and regard movement and fragmentation of land masses and the general immobility of plants and animals as major factors. The differences between the two viewpoints are more pronounced and complicated than suggested by this comparison (Nelson & Rosen, 1981; Pielou, 1981). It therefore seems important to clearly distinguish between the conceptual basis of the two theories and, for what I believe to be the first time, to present an outline of dispersal theory that fairly contrasts it to vicariance dogma. The fact that only vicariists have defined the limits of dispersal theory during the past decade has seriously distorted most biologists' concept of dispersal. Even such a perceptive scientist as Pielou (1981)

uncritically accepted the vicariists' terms for evaluation of dispersal theory, by following their lead in defining it as based upon long-distance dispersals that occur separately and independently in individual taxa. Perhaps some dispersalists (island biogeographers?) would concur. Most of those studying historical biogeography will not!

Some colleagues may question my qualifications for undertaking a balanced comparison of the alternate views, since my 1966 study of the Central American herpetofauna has a strong vicariance aspect (Fig. 2). Hopefully, their concerns may be laid to rest, since Croizat (1976) and Nelson (1977), commanders for the vicariists, characterize me as an ardent, but junior grade officer in the dispersalist army, who has dabbled in Neotropical biogeography. In any event, neither group is likely to be satisfied with my summarization of the central concepts of their preferred theory; the vicariists, because dispersal theory is shown to be very different from the distorted model they have created of it; the dispersalists, because of their diffuse variety of positions and general lack of parsimonious hypotheses for testing.

Both approaches to biogeographic theory construction recognize the occurrence of dispersal and vicariance events. Both are based upon recognizing and interpreting recurrent distribution patterns of many clusters of distantly related groups or organisms. Both have an evolutionary basis and are concerned with historical (phylogenetic) similarity. Both provide scientific models for the understanding of biogeography by addressing the following key elements: 1) recognizing congruent patterns of distribution; 2) analyzing these patterns to determine common ecologic, geologic, and/or evolutionary processes that produced the patterns; 3) using the patterns and processes to predict: a) patterns for yet unstudied groups and b) as yet undiscovered geographic and evolutionary events. The central conceptual framework of each approach is given below (Fig. 6):

Dispersal Theory:

A monophyletic group arises at a center of origin.
Each group disperses from this center.
Substantial numbers of monophyletic groups followed the same dispersal route at about the same time to contribute to the composition of a modern biota.
A generalized track corresponds to a dispersal route.
Each modern biota represents an assemblage derived from one to several historical source units.
Direction of dispersal may be deduced from tracks, evolutionary relations, and past geodynamic and climatic history.
Climate and/or physiographic change provide the major impetus and/or opportunity for dispersal.
Biotas shaped by dispersal across barriers and subsequent evolution in isolation.
Dispersal is the key to explaining modern patterns: related groups separated by barriers have dispersed across them: a) when the barriers were absent or relatively ineffective; b) less commonly by passing over or through existing barriers.

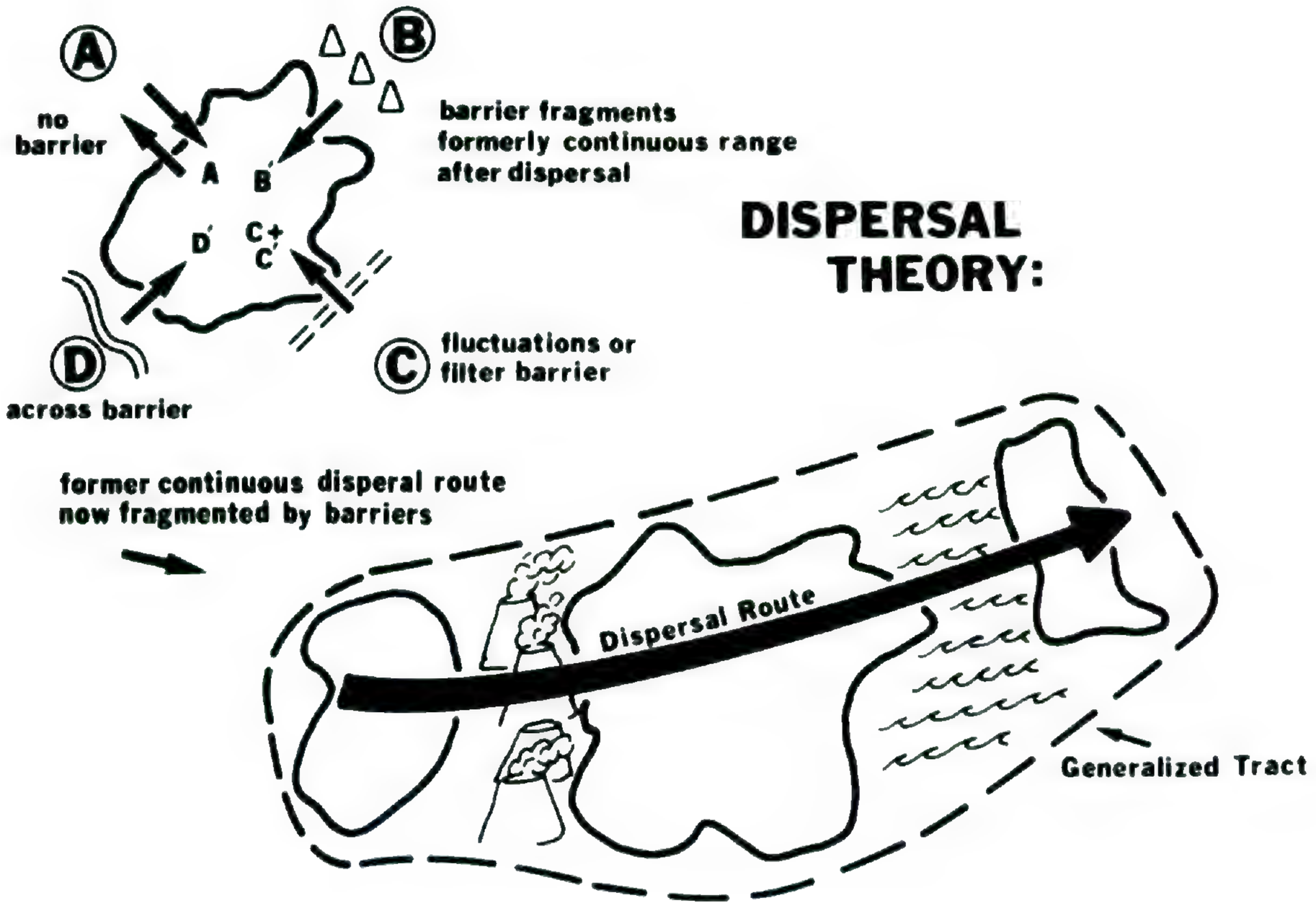


FIGURE 6. Essential features of dispersal and vicariance theories of biogeography.

Dispersal is of primary significance in understanding current patterns: dispersal precedes barrier formation and vicariance and again occurs when barriers are subsequently removed or become ineffective.

Vicariance Theory:

Vicariants (allopatric species) arise after barriers separate parts of a formerly continuous population.

Substantial numbers of monophyletic groups are simultaneously affected by the same vicariating events (geographic barrier formation).
A generalized track estimates the biotic composition and geographic distribution of an ancestral biota before it subdivided (vicariated) into descendant biotas.
Vicariance after geographic subdivision produced modern biotas.
Each generalized track represents a historical source unit.
Sympatry of generalized tracks reflects geographic overlap of different biotas due to dispersal.
The primary vicariating events are changes in world geography (geodynamics) that subdivide ancestral biotas.
Biotas evolve in isolation after barriers arise.
Vicariance is of primary significance in understanding modern patterns: related groups separated by barriers were fragmented by the appearance of the barriers.

The two approaches differ essentially in their emphases. In the dispersal model, associated organisms dispersed together to form the recurrent patterns. In the vicariance model, the original distributions are fragmented and the associated organisms in each fragment evolve together. Other key differences include:

Dispersal	*Vicariance*
1. Each monophyletic group has a center of origin from which it dispersed.	1. The ancestors of each monophyletic group originally occurred in the areas where the group occurs today and the descendant taxa now present evolved in place; center of origin not a valid concept (Croizat et al., 1974).
2. Concordant dispersal of many groups leads to patterns.	2. Concordant vicariance of many groups produce patterns.
3. Generalized track = dispersal route, used by a historical source unit.	3. Generalized track = ancestral biota (historical source unit).
4. Direction of dispersal deduced from track, phylogenetic relations, geodynamic and climatic relations.	4. Geological or geographical change causes biotic fragmentation.
5. Fossils very important; aid in locating center of origin and direction of dispersal; can contradict Recent distributions.	5. Fossils cannot contradict evidence from Recent distributions (Patterson, 1981); have no special role (Parenti, 1981).
6. Fossils aid in determining extinctions and phylogenetic age.	6. Fossils have no special role, since they do not invariably document ancestral biotas even when documenting extinctions (Parenti, 1981).

7. Discovery of new fossils tests biogeographic hypotheses.	7. Discovery of new fossils adds to track, but does not test or corroborate biogeographic hypotheses (Patterson, 1981).
8. Relative age of groups important in explanation; fossils important.	8. Age of group determined by vicariance pattern; fossils not necessary.
9. Ecologic valance and associates significant in analysis.	9. Ecologic valance and associates of little significance because they will correlate with ecologic and physiographic conditions of modern landscapes (Rosen, 1978).
10. Concordant dispersal occurs before establishment of barriers; isolation occurs after barrier formation (''Vicariance in disguise,'' Nelson & Platnick, 1978).	10. A primitive wide-ranging biota is fragmented by establishment of barriers.
11. Spatial (allopatry, parapatry, and sympatry) relations ambiguous.	11. Sympatry indicates dispersal; allopatry and parapatry indicate vicariance (Rosen, 1976).
12. Progenetic events involve concordant dispersal, and subsequent vicariance; epigenetic influences often equated with progenetic ones.	12. Progenetic events lead to fragmentation; epigenetic events produce details of current distributions (Rosen, 1978).
13. Ideas influenced by concept of constancy of ocean basins and permanency of continents: land and ocean areas stable, organisms dispersed.	13. Ideas strongly influenced by the new continental drift and (plate) tectonics: continents move, organisms carried passively with them.
14. Biotas dispersed along ecogeographic corridors with no or ineffective barriers or when barriers are removed.	14. Biotas carried on crustal plates or other geologic subdivisions; pattern reflects fragmentation brought about by origin of barriers.
15. Ideas influenced by mammal data as interpreted by Matthew and Simpson: dispersal from northern continents to southern ones.	15. Ideas influenced by data for fishes as interpreted by Nelson and Rosen: fish groups are old enough to have been affected by the breakup of Pangaea.
16. Often a heavy emphasis on Quaternary events as sufficient to explain patterns through ecologic correlations (Müller, 1973; Haffer,	16. Major patterns represent ancient (Mesozoic onward) disjunctions; speciation events generally pre-Quaternary.

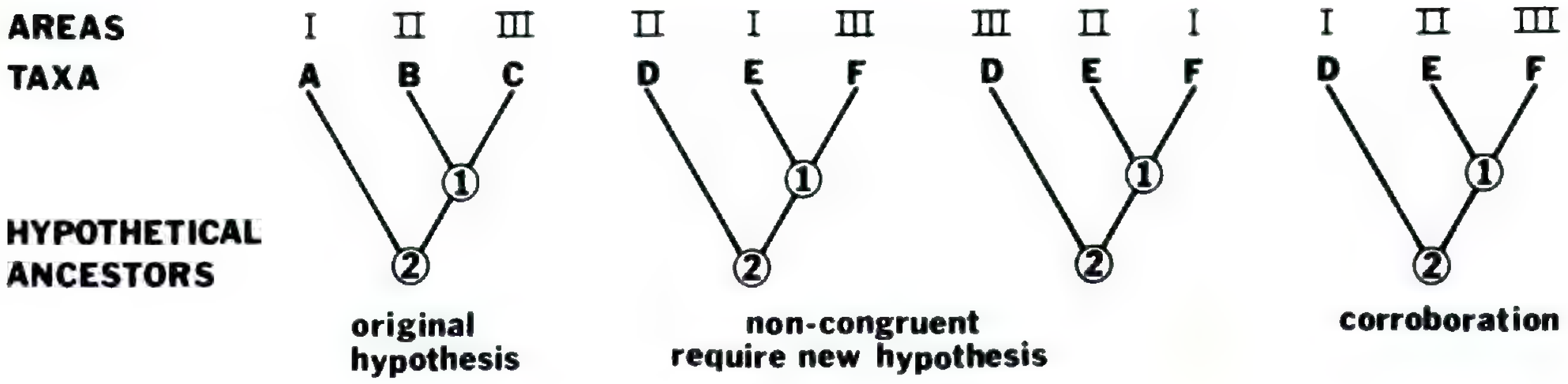
1981); sometimes even shorter time frame emphasized (MacArthur & Wilson, 1967; Simberloff, 1974; Cody & Diamond, 1975).	
17. Components (nodes) in generalized track equal minimum number of dispersal events.	17. Components (nodes) in generalized tracks equal minimum number of vicariance events.
18. Hypotheses tested adding additional individual tracks; corroborated if conform to dispersal routes; falsified if incongruent.	18. Hypotheses tested by adding additional individual tracks; corroborated by congruence; falsified by incongruence.
19. Lack of conformity with well-documented generalized and/or component tracks: a) individual track represents dispersal of another historical source unit; b) the individual track reflects independent long-distance dispersal; c) the individual track is based on a non-monophyletic group.	19. Lack of conformity with well-documented generalized and/or component tracks: a) the individual track belongs to another generalized track; b) the members of the individual track have broken away from the parent biota and have independently dispersed; c) the individual track is based on a non-monophyletic group.
20. Hypotheses tested by comparing proposed number of major dispersals with geologic, physiographic, ecologic, and climatic changes.	20. Hypotheses tested by comparing proposed number of vicariance events with geologic history.
21. Predicts some geologic, physiographic, and climatic events, but these are usually highly correlated with recent conditions; does not distinguish among effects.	21. Predicts geologic history (Rosen, 1976, 1978).
22. Predicts patterns for unstudied groups of same age.	22. Predicts patterns for unstudied groups.
23. Need some initial notion of age of groups, timing of geologic and climatic events and centers of origin.	23. No prior judgement of former history of dispersals or geologic ages of distributional events; these discovered by the analysis.
24. Eclectic analytical method: equal weight to original historical patterns, dispersals, climatic effects, evolution *in situ* and interrelationships; final arbiter, paleontology (Keast, 1977).	24. Robust analytical method: construct cladograms of areas that are tested by cladograms of relationships for individual taxa; geologic history is final arbiter (Rosen, 1978; Nelson & Platnick, 1978).

As shown by the wide range of evidence and explanation in the Vicariance Biogeography Symposium held in New York City in 1979 (Nelson & Rosen, 1981), the debate between and among dispersalists and vicariists goes on (Pielou, 1981) and will probably continue to do so for sometime. The vicariists show some tendency to back away from earlier rigid theoretical formulations through: a) recognition that generalized tracks are phenetic measurements of overall similarity between disjunct or adjoining biotas; b) consideration by implication of the possibility for the existence of second order vicariance events besides those caused by the major forces of earth history, i.e. sea-floor spreading and drifting tectonic plates (Rosen, 1978; Platnick & Nelson, 1978); c) recognition that cladistic analyses of the interrelationships of areas does not equivocally distinguish between vicariance and concordant dispersal (Morse & White, 1979); d) concession that fossils are useful in documenting extinctions and giving minimum ages for occupation of areas (Patterson, 1981); and e) realization that dispersal events and differential extinctions obscure the picture established through vicariance (Patterson, 1981). The dispersalists, on the other hand, remain in disarray, since in most cases, their narrative explanations tend to be overly complicated (non-parsimonious) and rarely subjected to rigorous analysis. In other words, most dispersal hypotheses treat individual cases and do not provide a general explanation of pattern.

Probably the most important recent trend in vicariance biogeography has been the concentration on development of a methodology to evaluate the interrelationships among areas (see item 23 above), since distributional data seem insufficient to resolve whether dispersal or vicariance is the cause of particular disjunct or adjoining patterns of distribution. The methodology, as proposed by Platnick and Nelson (1978), generalized by Morse and White (1979) and utilized by Rosen (1978) and Patterson (1981) requires a detailed cladistic analysis of a number of monophyletic groups for a particular region. These hypotheses of interrelationships among taxa are then converted to a cladogram of areas that expresses a hypothesis concerning the interrelationships between biotas. Additional congruent taxon cladograms may corroborate the general pattern of area relations. In that event, a review of the geologic history of the region may allow specification of a sequence of events that correlates with the interconnections and subsequent sequential isolation of areas. If additional taxon cladograms are non-congruent with the original hypothesis of area relations (because of non-concordant dispersal or the presence of another general pattern of area relations), a new hypothesis or hypotheses need to be formulated for further testing (Fig. 7).

The method is further restrictive as emphasized by Nelson and Platnick (1979) in that the only informative taxa are those with endemic representatives in each of three or more areas. Widespread taxa (i.e. those found in two or more areas) are regarded as the equivalents of shared primitive characters in systematics (non-informative). Congruent cladograms of individual taxa occupying the areas are equivalent to shared derived features in systematics and I suppose that unique endemic taxa are analogous to unique features.

If the comparison to cladistic systematics is extended, this biogeographical method aims at interpreting the geographic distribution of "sister groups" parsimoniously (Patterson, 1981). It asks whether there is a single cladogram of areas



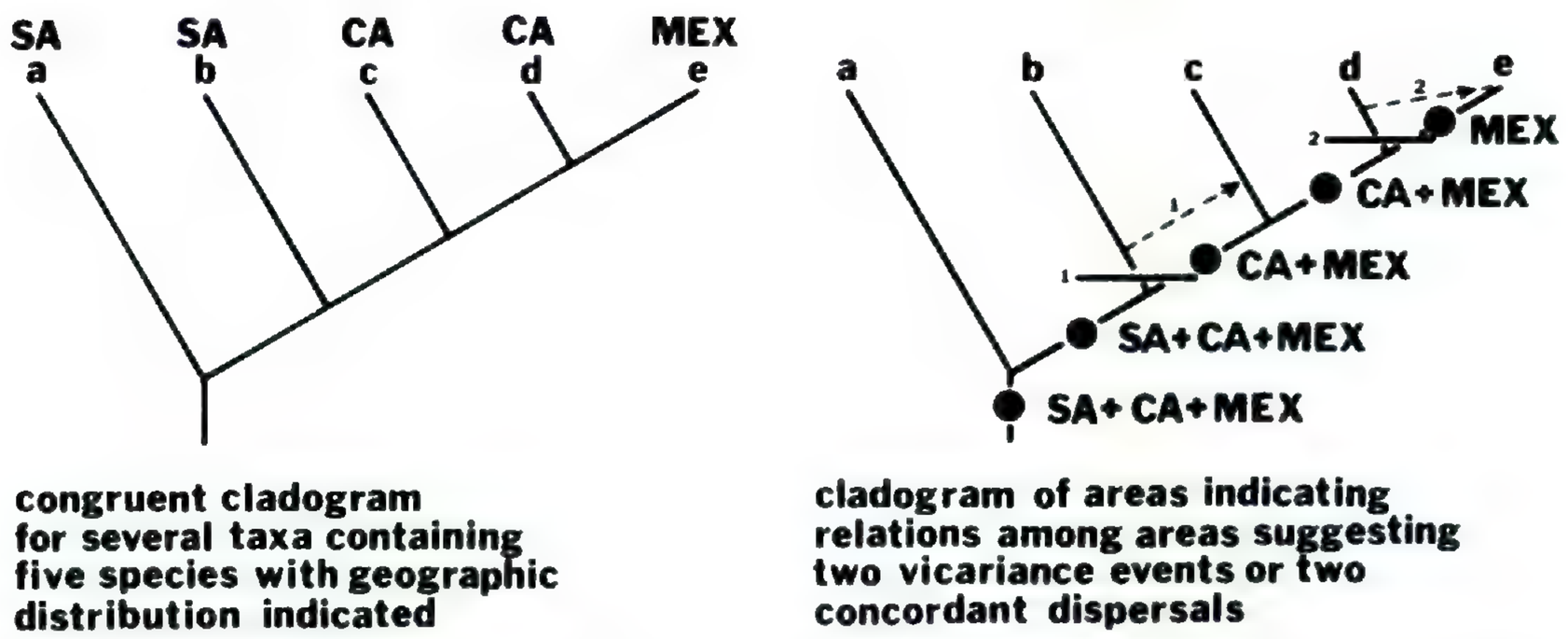


FIGURE 7. Evaluation of interrelationships among areas. Upper, phylogenetic relationships form a hypothesis of area (I, II, III) relationships to be tested by additional phylograms; arabic numbers (1–2) denote hypothetical ancestors and/or ancestral distributions. Lower, phylogenetic relationships form a hypothesis of geographic interrelationships; dispersal theory requires two dispersals for explanation, vicariance theory assumes a single widespread ancestor in South America (SA), Central America (CA), and Mexico (MEX) fragmented by two major vicariance events.

(or more than one) that summarizes the interrelationships of endemic taxa of the groups found in a region. If the intra-group relationships of the distributions of a number of taxa are congruent, then a general explanation is sought. If the relationships are non-congruent, independent long-distance dispersal seems likely. If two or more congruent patterns emerge, then there are two or more general explanations that must be correlated among known geological, geographical, and ecological events to assess actual causal relations. Contrary to the expectation of Patterson (1981), discovery of a general congruence of distributions cannot discriminate by itself concordant dispersal from vicariance (Morse & White, 1979).

This method has been applied in actual cases only to upper Mesoamerica (Rosen, 1978) and marsupials (Patterson, 1981), although several other studies of its application are in preparation. Although Pielou (1981) questions its effectiveness and scientific rigor, it appears to have great potential when sufficient cladistic analyses of taxa are available for a region. At the present time, we may conclude that the method has not been proven by adequate testing and that its restriction to a three or more endemic taxa comparison, the elimination of wide-spread taxa from consideration, the subsidiary use of fossils, and the failure to specify how to distinguish concordant dispersal from vicariance without reference to geologic history, limit its applicability, since it only resolves the pattern of interconnec-

tions among areas. A general pattern of area relations may, however, be ascribed to dispersal or vicariance by the use of the independent test of earth history (Platnick & Nelson, 1978). The absence of a sufficient number of cladistic analyses of taxa for Central America, especially, forces me to utilize another approach in the analysis and synthesis present in the subsequent sections of the paper. The method of Platnick and Nelson (1978) and Rosen (1978) should be an effective test of my conclusions as more cladistic analyses become available.

HISTORICAL UNITS OF THE HERPETOFAUNA

In my 1966 report, I utilized what are now called by vicariists traditional and/or conventional methods of correlative evaluation of present distribution, ecologic associations, the meager fossil record, phylogenetic relationships, and the association of herpetofaunal units with geofloral history to develop a narrative (sensu Ball, 1976) theory of herpetofaunal development. Essential to that theory were the recognition of herpetofaunal source units using the method described in an earlier study (Savage, 1960). The narrative theory consisted of a description of the *in situ* development in, or the concordant dispersal into, Central America of the taxa belonging to each unit.

As outlined in the immediately preceding section, the generalized track method (Croizat, 1976; Rosen, 1976) may be used as a basis for estimating patterns, regardless of biogeographic theory. Since this method was not used in my earlier study, it seemed that it might be applied to the herpetological data to see if it produces independently similar or distinctly different results than previously obtained. This seems an especially good idea because of questions raised concerning my interpretation of herpetofaunal distribution for the region as outlined in an earlier section (A Review of the Problem).

The generalized track method as used in vicariance biogeography is described in detail by Rosen (1978: 432–433). In summary, the method consists of outlining the distribution of disjunct or adjoining taxa of several to many monophyletic groups on a map and linking the distributional areas of each group by an all-encompassing circle or a line (track). Where commonality of distribution occurs, lines that repeatedly link sister groups will form a single massed pathway called a generalized track. Distinct clusters of distributions (nodes) within the generalized tracks form component tracks tied together by the more general pattern. Although claimed by vicariists to be a significantly different method of pattern recognition, construction of tracks differs in no significant way from the methods used by conventional biogeographers, i.e. overlaying the distribution maps of many groups, to establish patterns.

In vicariance biogeography, generalized tracks are assumed to link two or more vicariant fragments of an ancestral biota. It is further assumed that there is a general explanation of the congruence of the distributions of taxa within a track. The congruence is then explained by correlative or causal relations between earth history and the fragmentations.

The tracks seen by most dispersalists correspond to corridors of present or past concordant dispersal, whose directionality may be estimated from the phylogeny of the groups, and a knowledge of climatic, ecologic, and geologic rela-

tionships. In essence, the dispersalists take the generalized track of the vicariists and put an arrow at one or both ends to indicate the directionality of dispersal.

Ball (1976), McDowell (1978), Patterson (1981), and Pielou (1981) are critical of the value of the use of the generalized track method in vicariance theory because it is phenetic. By that, they mean that a generalized track measures overall similarity in distribution but obscures evolutionarily based similarities through the biogeographic equivalents of convergences (recent and/or long-distance dispersals by individual taxa). As such, they argue that generalized tracks cannot point to a single general explanation of coincident distributions. Why is this so? Tracks tend to follow current physiographic and ecologic trends. For many groups of organisms, the tracks represent an ancient relationship that may indeed be interpreted in terms of vicariance events and an association with the areas involved that predates current physiography and ecology. In other cases, this ancient pattern may be overlain by group distributions that appear to conform to the same general track but represent a more recent concordant dispersal event. Finally, rather recent individual dispersal events may add a distribution to the track that appears to conform to the ancient pattern.

Within the context of dispersal theory, generalized tracks correspond to dispersal routes. Since modern biotas are regarded in this view as derived from several source units (not as a single fragment of one track), the biotas are phenetic units equivalent to overlapping nodes representing several different generalized tracks. In this regard, dispersalists believe that different source units may have utilized more or less the same dispersal route at different times in geologic history depending upon barrier relationships. Dispersalists, generally speaking, see a modern biota as comprised of the components of several historical units, derived at different times from several sources, but usually dominated by a source unit that has developed *in situ* (Fig. 8).

It should be mentioned that Rosen (1976), in his analysis of Caribbean biogeography, breaks with orthodox vicariance dogma to suggest that several generalized tracks with temporally different histories have contributed to the modern Central American and Antillean biotas.

A final set of problems with the use of generalized tracks by vicariists, as pointed out by McDowell (1978) and Pielou (1981), lies with the reliability of the method of track construction and at what point sufficient congruent individual tracks are accumulated to recognize a generalized one. For example, if one looks at Rosen's (1976) carefully researched and documented South American-Caribbean track, it can immediately be extended by additional groups that conform to the track, but are distributed well to the north. Similarly, the track may be substantially extended to the south, to make the track cover most of the Americas (Fig. 9). Very likely by judicious choice of monophyletic groups, the generalized track could be extended to Africa and elsewhere. By the same token, while many monophyletic groups of taxa will fit the originally proposed track, some others do not. Despite the claims of Croizat et al. (1974) and others, the mere coincidence of a number of tracks does not test the reality of the track. Coincidence merely corroborates the hypothesis that a track exists. The vicariist track then is an empirical construct of pattern that invites explanation and cannot provide an explanation, itself.

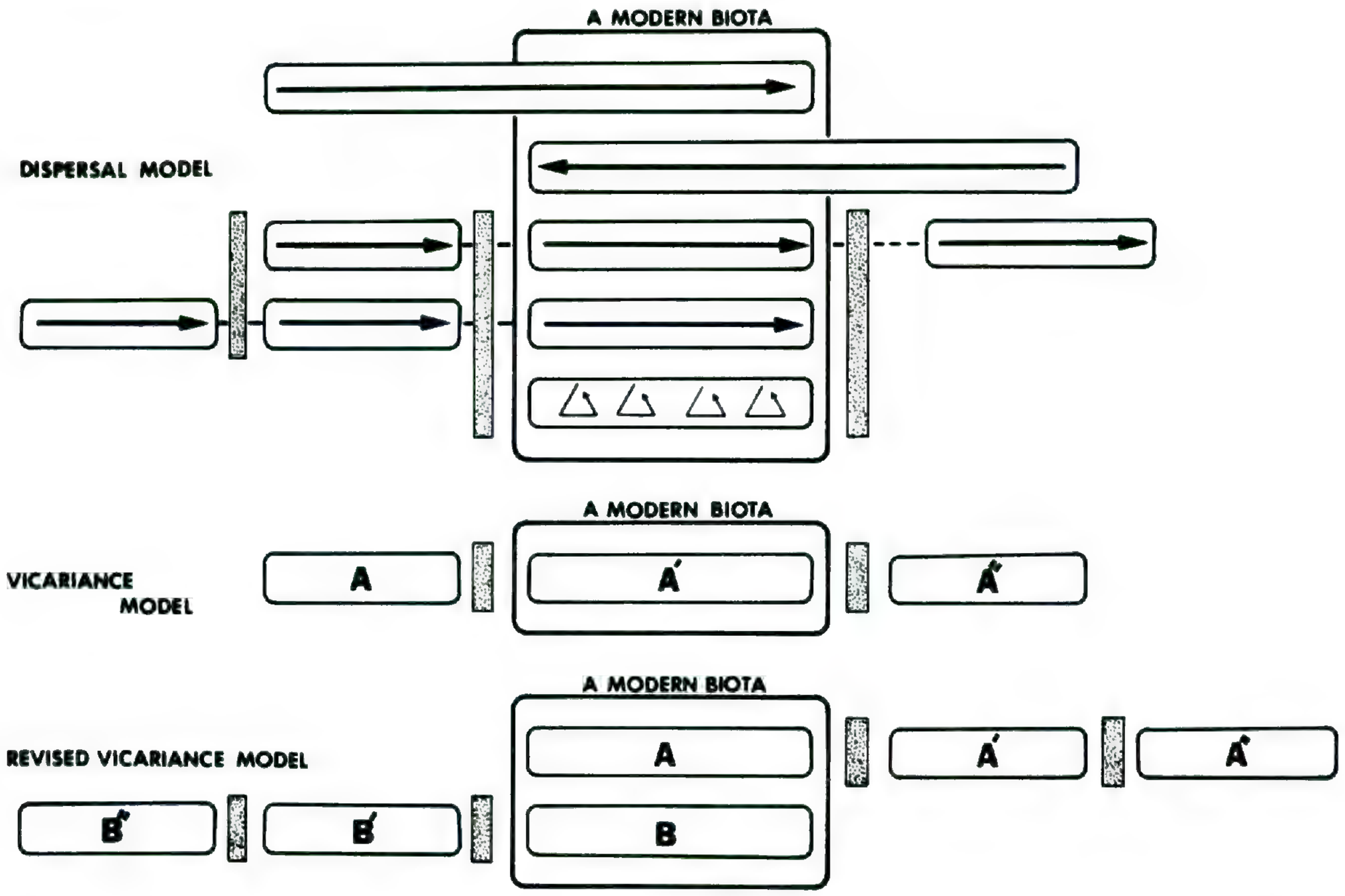


FIGURE 8. Generalized tracks and biotas. Upper, dispersal theory, with several tracks (= dispersal tracks) or historical units contributing to a biota. Lower, vicariance models. Stippled bars represent barriers, small arrows *in situ* differentiation.

With the realization that generalized track analysis was founded on a phenetic basis, vicariance theoreticians shifted ground to identifying areas of endemism as the basis for analytical study of patterns (Rosen, 1978; Platnick & Nelson, 1978). In doing so, they raised four important questions that are to be asked in the biogeographic analysis of a region: 1) What are the areas of endemism (we already known that they are geographically non-random)? 2) Do the interrelationships of the endemic taxa form a geographically non-random pattern(s)? 3) Does the pattern(s) correlate with geologic history? 4) If the answer to 3 is yes, can a causal hypothesis be established? (Nelson & Platnick, 1978). The method for undertaking this analysis has been outlined in an earlier section of the present paper.

This approach requires a reversal of traditional biogeographic analysis, where much emphasis has been placed upon taxa shared in common. The conventional wisdom is that biotas that have the most taxa in common are most closely related to one another (Vuilleumier, 1975). As an example, comparison between biotas I, II, and III might result in the conclusion that II and III are more closely related to one another than either is to I, because they share more taxa in common than either does with I (Fig. 10). It is easy to accept what is accurately perceived by the vicariists, that wide-ranging taxa, those shared by all areas (three in this case) in a region provide little information on interrelationships of biotas. Essentially, widespread or shared taxa inform us only that there *is* a relationship among the

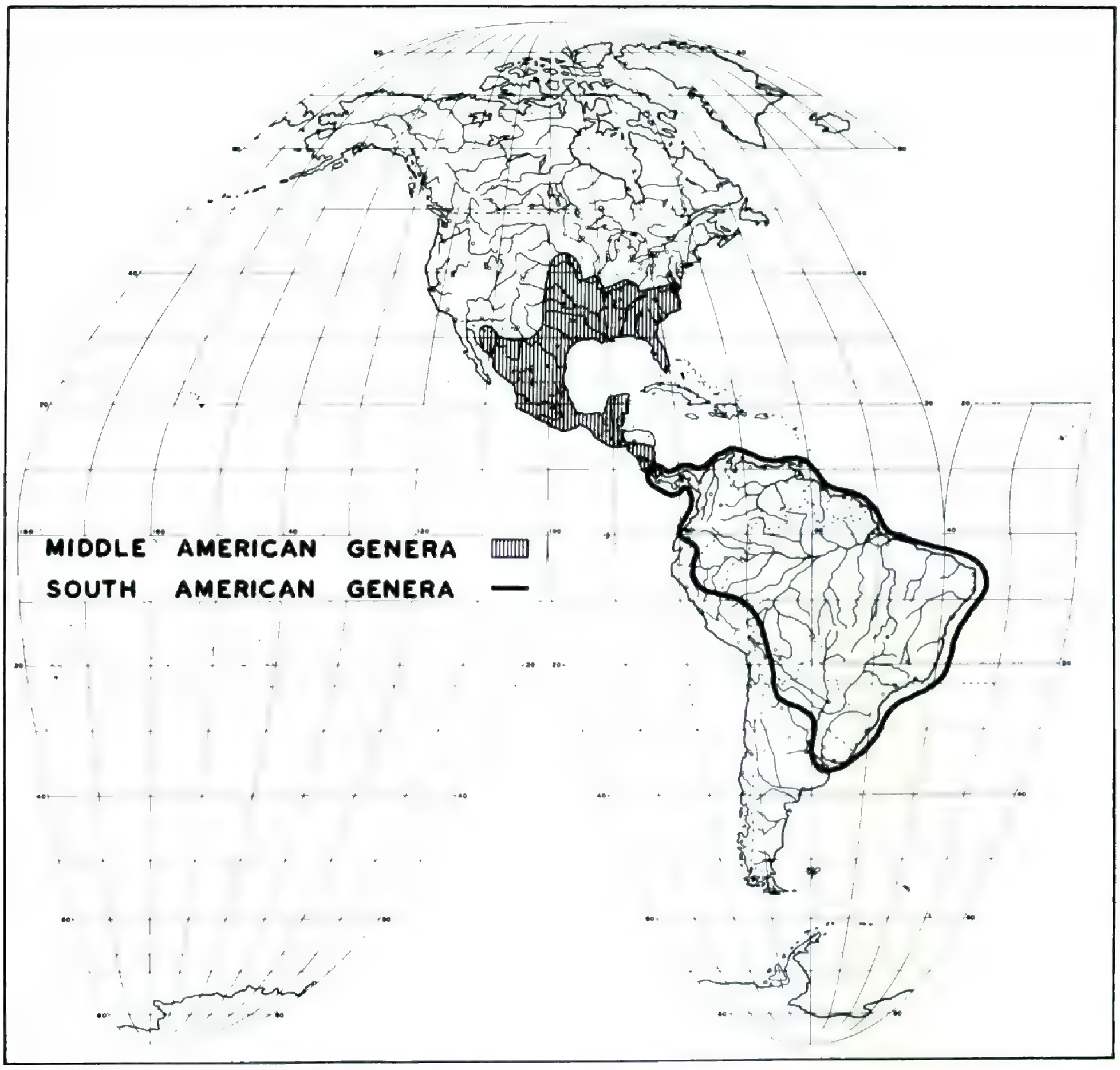


FIGURE 9. Distribution of microhylid frogs in the Americas, showing discreteness of northern and southern fragments and correspondence with the extension of Rosen's (1976) South American-Caribbean generalized track.

areas, since they correspond to primitive shared characters in evolutionary analysis. What is not so easy to see is the vicariists' brilliant insight that taxa shared by any two of three areas are equally irrevelant to the question of interrelationships, since the same two historical events may produce a situation where any two taxa may be shared by any pair of the three areas (Fig. 11). It is for this reason that a minimum of three areas of endemism, each characterized by an endemic species, are required for vicariance analysis at this level. As pointed out earlier (Fig. 7), an initial hypothesis relating to interconnections or dispersals between the areas may be generated when two (or more) sets of endemic taxa are found to be area congruent in their phylogenetic relationships.

What then of the criticism that this methodology discards important or significant data, the distribution patterns of widespread forms? A widespread taxon in the region, under study, can be utilized as an endemic when the region is compared to two or more other areas having endemic sister taxa and will con-

tribute to understanding the hierarchial pattern of regional relationships. As in cladistic analysis of the interrelationships of taxa, what is a shared primitive character at one level of analysis of the hierarchial pattern of evolutionary novelties, must represent a shared derived feature for another more-encompassing unit.

Because of the emphasis in the vicariists' approach on areas of endemism, most dispersalists will be surprised to learn that comparisons of the relative number of endemics among areas provides little information on their interrelationships (Nelson & Platnick, 1981: 398–409, for a stunning *denouncement* of this old idea). Indeed, it sometimes turns out that two endemics out of a hundred are more informative than 82 endemics out of a hundred (Fig. 10).

GENERALIZED TRACKS AND AREAS OF ENDEMISM

With the difficulties of generalized track analysis and the enhanced significance of areas of endemism in mind, we may now turn to a review of these matters as discerned in the Central American herpetofauna. My concept of generalized tracks is of a pattern of distribution giving initial phenetic clues as to past distributional events. Metaphorically, a generalized track is a trace marked on the earth's surface of ancient dispersal and vicariance events. As mentioned above, track analysis may be obscured by coincidence with the track of several different concordant dispersals in different time frames, rather recent individual dispersal events, and overlapping of two or more generalized tracks. Nevertheless, track analysis seems to afford a method for proposing initial hypotheses regarding the historical source units in a region.

Areas of endemism may be regarded as indicators of significant vicariance events that fragmented previously continuous ranges or as the products of concordant dispersal followed by vicariant evolution. Areas of endemism form nodes of differentiation connected by generalized tracks. Metaphorically, generalized tracks may be thought of as a string of pearls, with the centers of endemism represented by the pearls and the record of past events by the connecting string. The pearls may be closely packed, widely spaced, or of mixed pattern, but they hang together because of the string. Just as several strings of pearls of similar or different length may be worn at the same time, several generalized tracks may overlap. In the final analysis, the richness of the effect or the biota is the result of the total visual impact or the general pattern, respectively, produced by the juxtaposition of the strands of pearls.

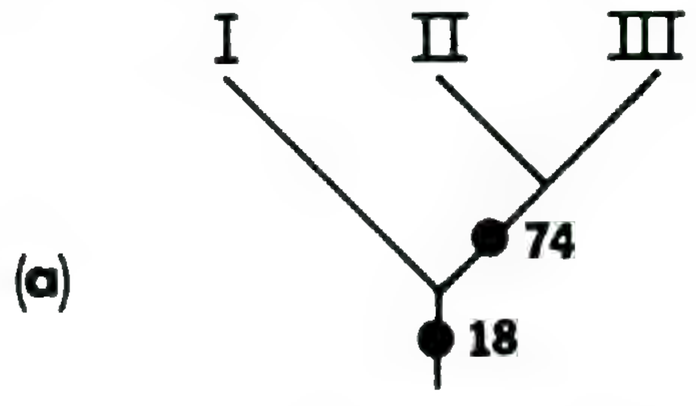
For purposes of this study, individual tracks of all genera and a few subgeneric groups that occur in tropical Mesoamerica were constructed. Component generalized tracks within the region were recognized as repeated nodes of congruent distributions. Whenever monophyletic allies of Mesoamerican groups were known to occur elsewhere, their ranges were plotted and joined in a generalized track, including regional and extraregional components. An initial assumption was made that congruent distributions represented a shared history of concordant dispersal or vicariance.

It was expected that, because of the complex history of the region, a single generalized track might simultaneously contain an overlay of recent dispersal

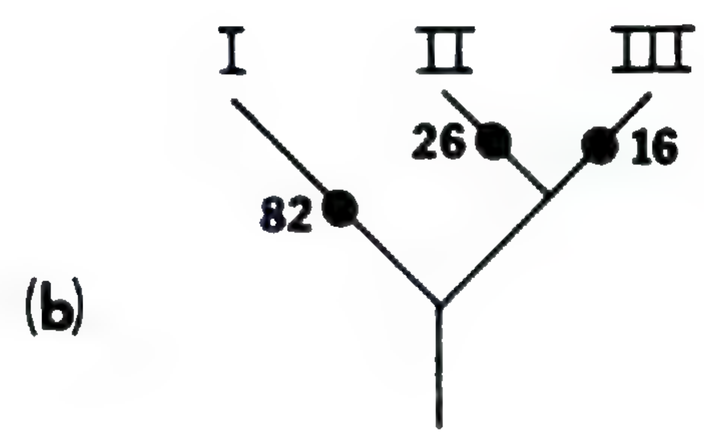
THREE AREA COMPARISONS

AREA:	I	II	III
ENDEMICS:	82	16	26
SHARED TAXA	I-II	I-III	II-III
	18	18	74

AREA RELATIONSHIPS (AREA CLADOGRAMS) METHOD OF TAXA IN COMMON



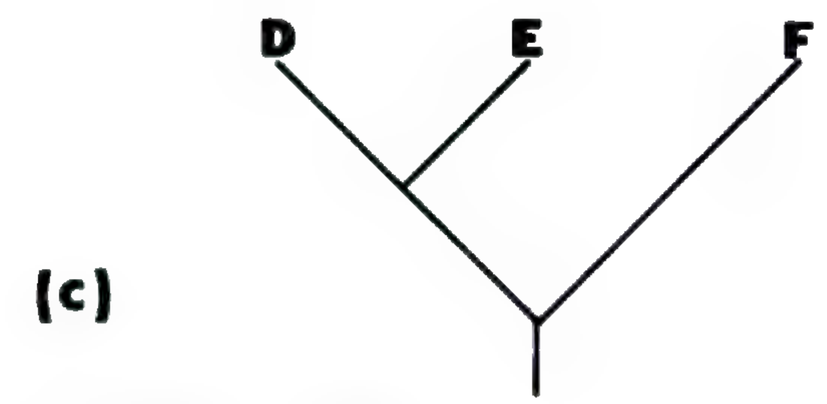
METHOD OF RELATIVE NUMBER OF ENDEMICS



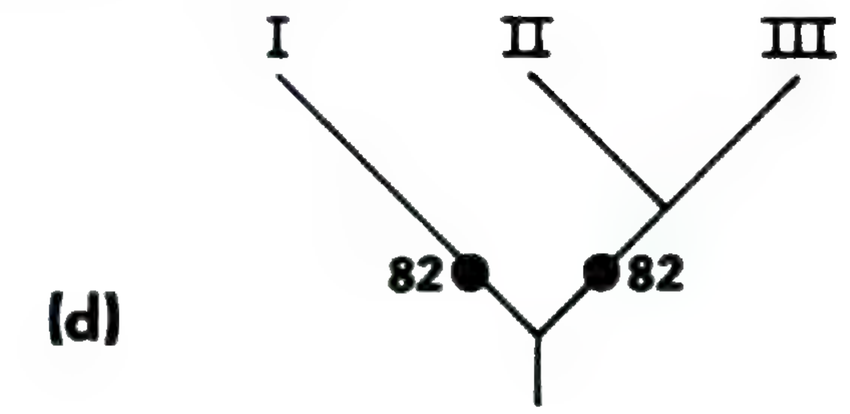
VICARIIST METHOD

In the studied areas two series of 3 endemic taxa (ABC and DEF) show these relationships (only sets of related 3 area endemics)

AREA	I	II	III
SERIES	A	B	C
SERIES	D	E	F



Other taxa related as follows:



Which of the four cladograms best expresses historical relationships?

Most will say a b d (conventional), nevertheless, it is c, (vicariist)

FIGURE 10. Why biotas with the most taxa in common are not necessarily the most closely related (a). Why the relative number of endemics among areas (b) provides little information on area relationships. Why phylogenetic relationships of three endemics in three areas (c) are more significant than relationships among 82 other taxa (d).

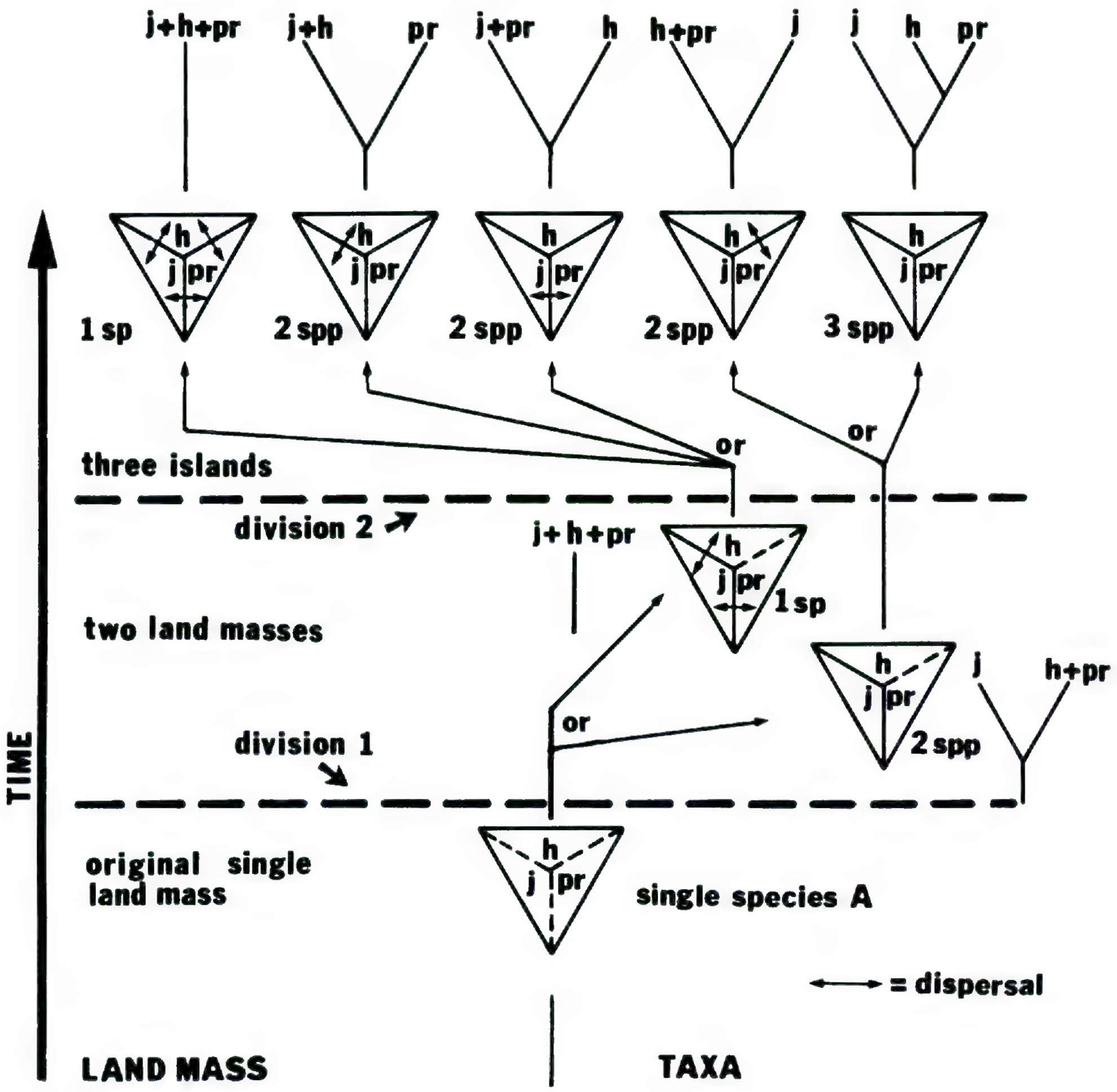


FIGURE 11. Explanation of why taxa shared by two areas in a three area comparison are relatively uninformative concerning area interrelationships. In this example there are three different ways in which two of three islands may share the same species; only when each area has an endemic (3) can area relationships be determined.

events and evidence of an ancient interconnection between components, which would obscure the patristic biogeographic relationships. Since dispersal events are of two general types, individual and concordant, both possibilities needed to be considered and eliminated from construction of the generalized tracks. The following paragraphs introduce a method for these purposes. The method does not eliminate the possibility of long-distance dispersal by individual taxa joining and sharing a track. However, it does eliminate them from the process of track construction.

The method is as follows:

1. Any species that had a more or less continuous distribution involving a substantial area in extratropical North, Central, and South America was

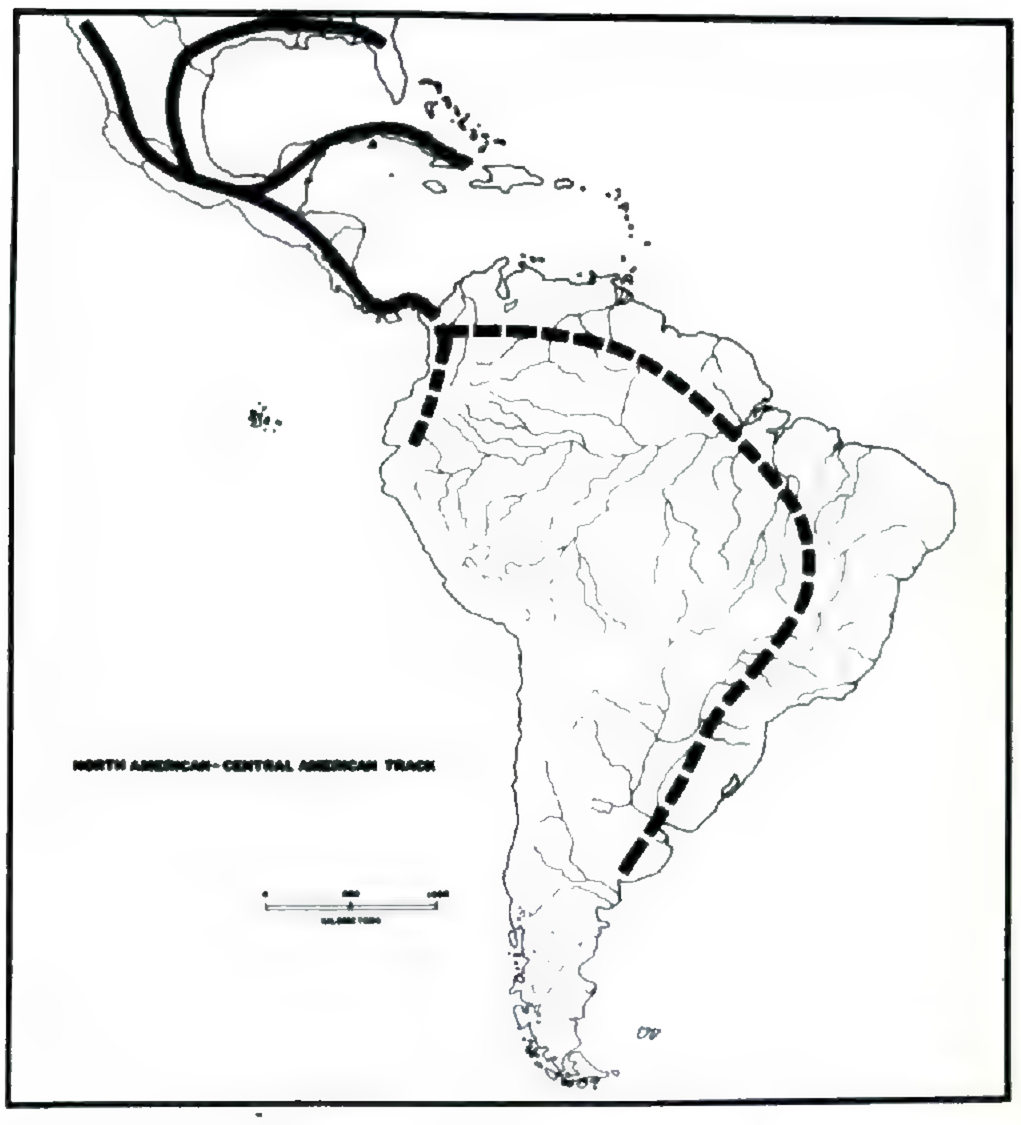


FIGURE 12. Generalized North American-Central American Track; dotted portion indicates post-Miocene dispersal across Isthmian Link.

eliminated from initial analysis (e.g. the indigo snake *Drymarchon corais*, which ranges from Florida to Uruguay).

2. Where a group has an area of differentiation in South America and one or two wide-ranging forms with more or less continuous geographic ranges extending a limited distance into Central America, or vice versa, this was interpreted tentatively as dispersal across the Isthmian Link during its pe-

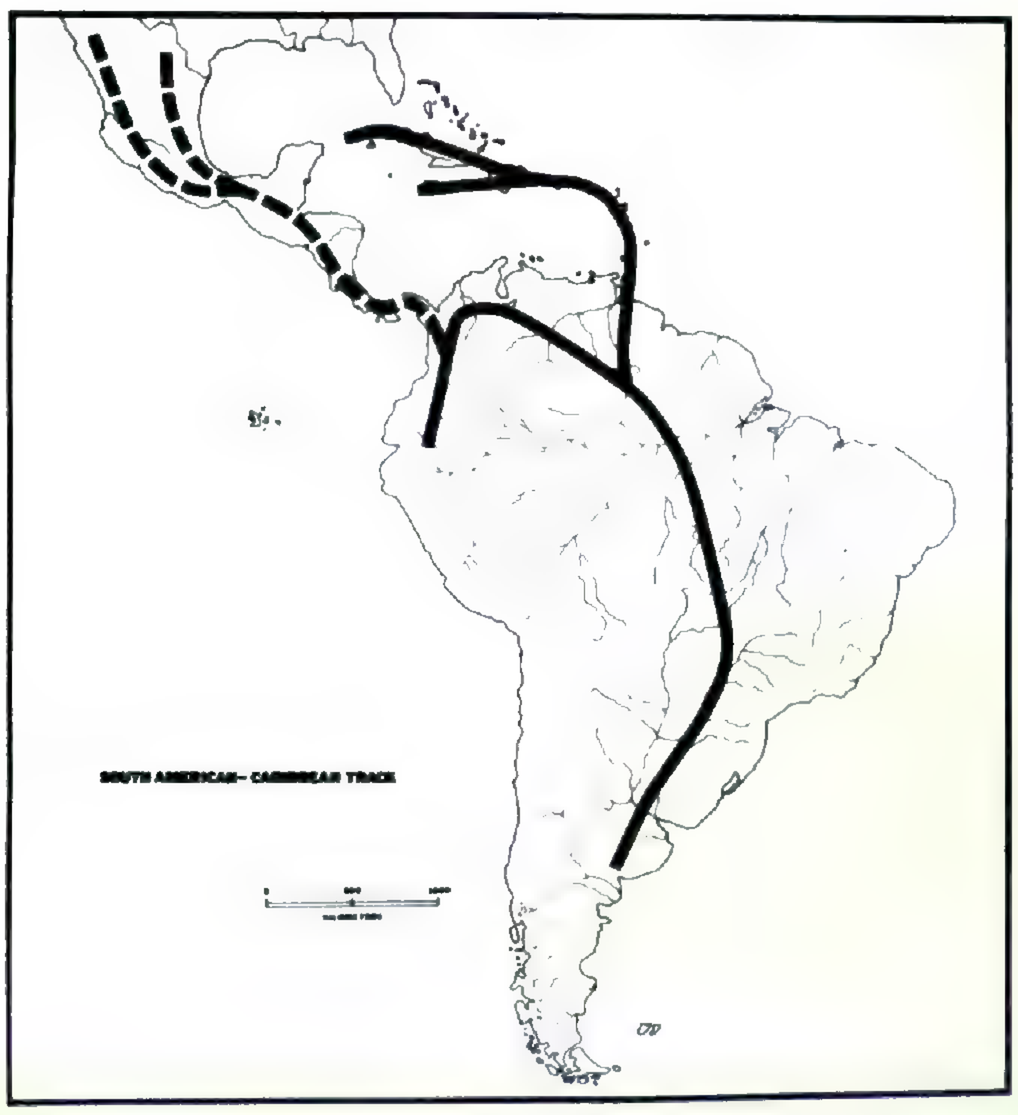


FIGURE 13. Generalized South American-Caribbean Track; dotted portion indicates post-Miocene dispersal across Isthmian Link.

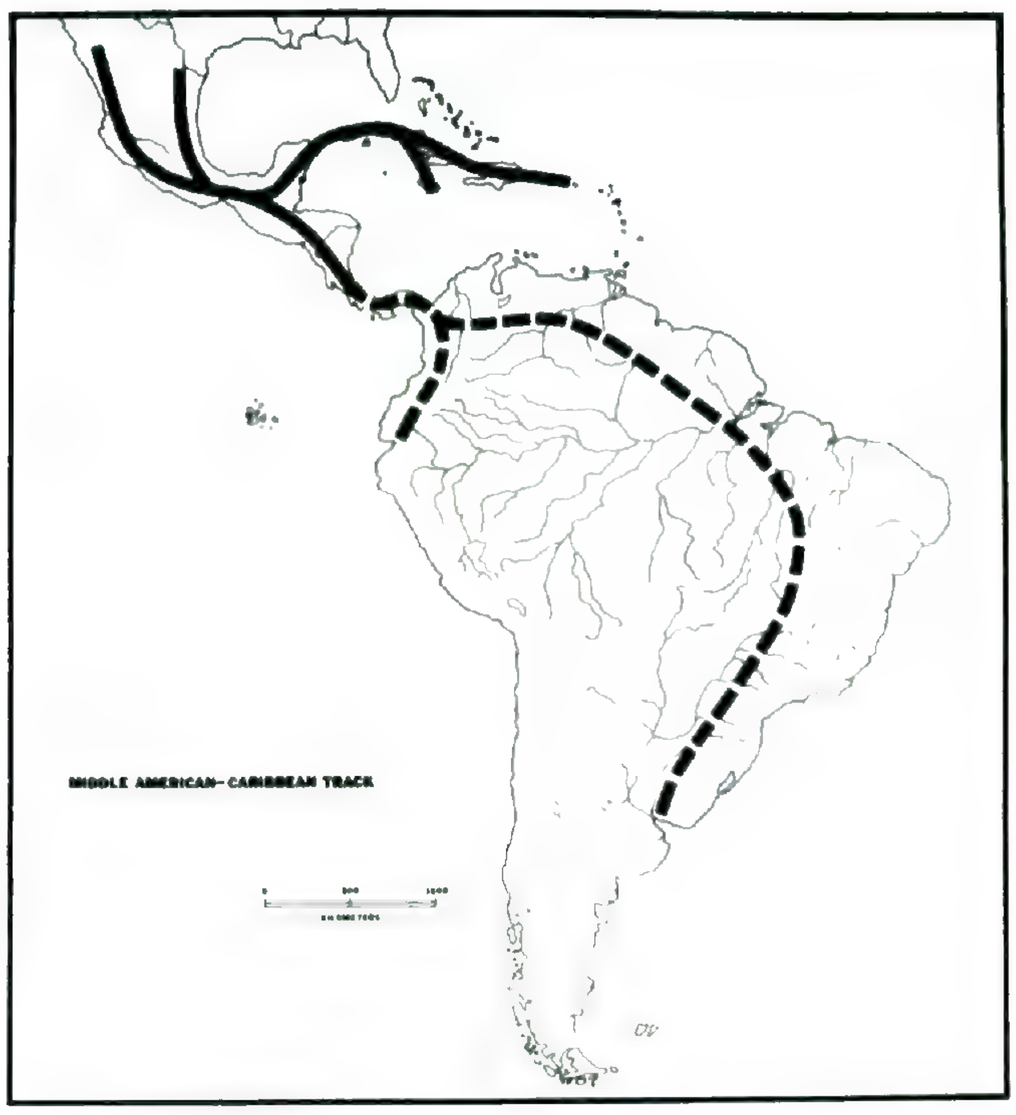


FIGURE 14. Generalized Middle American-Caribbean Track; dotted portion indicates post-Miocene dispersal across Isthmian Link.

riod of emergence (the past 5–3 million years); these groups were eliminated from establishing the track (e.g. the family Dendrobatidae, which is primarily South American, but ranges north to southern Nicaragua).

3. Whenever possible, the fossil record of group history was used to test the tentative decision from 2, since the presence of the group or a close ally in both North and South America prior to the formation of the Isthmian

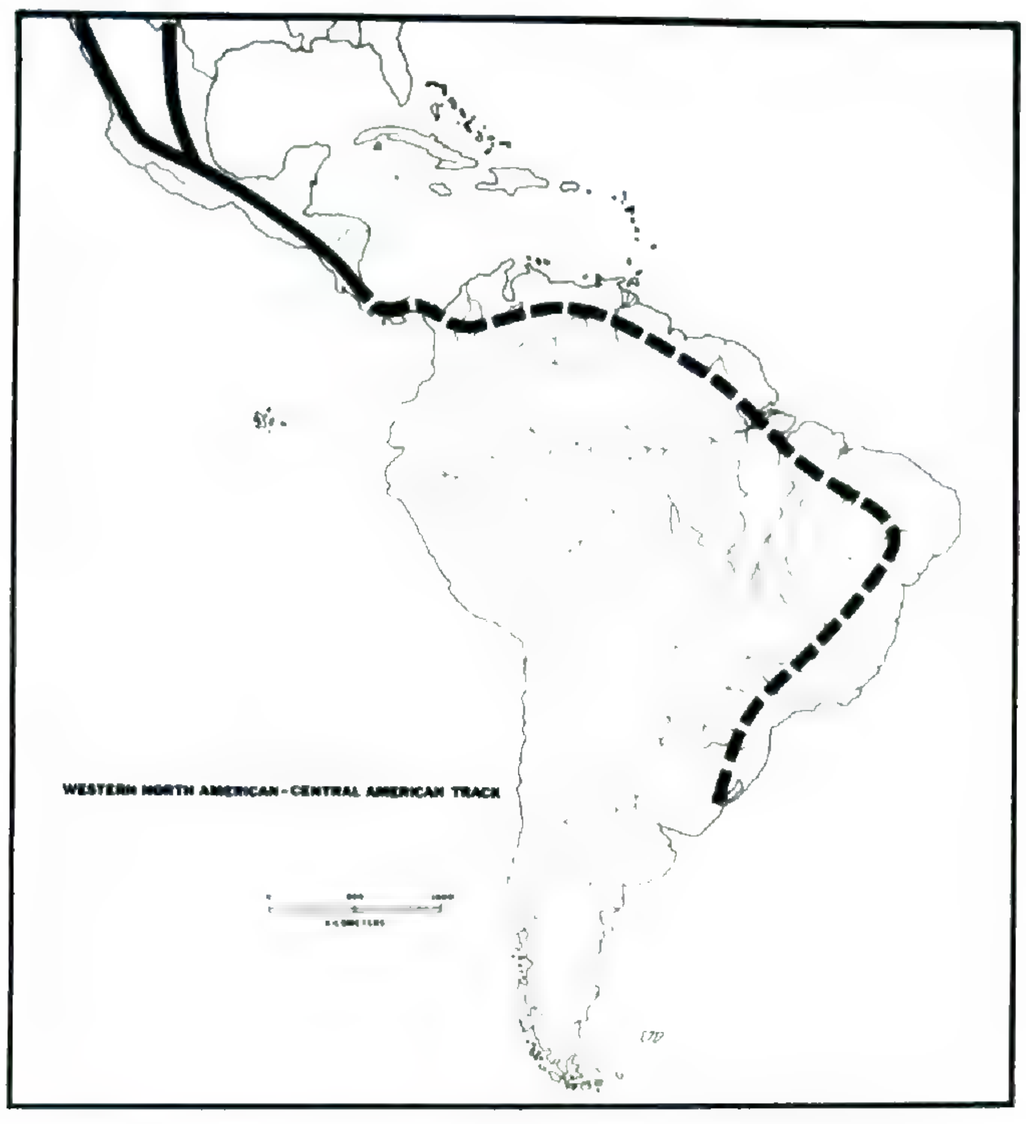


FIGURE 15. Generalized Western North American-Central American Track; dotted portion indicates post-Miocene dispersal across Isthmian Link.

Link would falsify the conclusion that the group had dispersed across the present Isthmus; the group and its fossil allies could then be added to a track; the contrary situation where the group and/or its fossil allies are known from one region (e.g. North America), but not the other (South America), would support the initial hypothesis of post-Miocene dispersal (e.g. the iguanine lizard *Iguana* in both Central and South America, all other mainland genera in the group have fossils from North and Central America).

4. The appearance of several sympatric generalized tracks in the analysis will disclose potential concordant dispersal events.
5. Groups originally eliminated from the process of establishing tracks may be identified with a track by subsequent comparison of phylogenetic relationships and fossil data (e.g. *Drymarchon* is a member of an essentially North American stock of colubrid snakes, unknown in the fossil record of South America).

Based upon a review of the distributions of the genera of amphibians and reptiles in Central America, according to these principles, three major and one minor (comprised of a relatively few taxa) tracks may be recognized:

1. The North American-Central American track is a generalized track that includes North America, the Mexican lowlands and montane uplands, Central America, and the Greater Antilles (Fig. 12). South American portions of this track extend to Ecuador and Argentina but represent dispersal after the reconnection of Central and South America in the Tertiary.
2. The South American-Caribbean track is a generalized track including South America, the Greater and Lesser Antilles and the Bahamas (Fig. 13). Mexican and Central American portions of this track represent dispersal from South America after establishment of the Isthmian Link in the Pliocene.
3. The Middle American-Caribbean track is a generalized track including the lowlands of Mexico, Central America and the Greater Antilles and the Bahamas (Fig. 14). The portions of this track that extend to Ecuador and southern Brazil represent post-Miocene dispersal across the Isthmian Link.
4. The Western North American-Central American track is a generalized track including western North America, Mexico and Central America, north of Panama (Fig. 15). A portion of this track, extending into South America, represents the dispersal of two genera (*Cnemidophorus* and *Crotalus*) across the Isthmian Link in late Cenozoic, followed by differentiation into a few species, each.

Descriptive and phenetic, generalized tracks represent empirical repetitive patterns of distribution that need biogeographic explanation. In both dispersal and vicariance biogeography, the patterns require that we seek explanations that are concordant with the phylogenies of the taxa and with earth history. Identification of areas of high endemism forms a further useful aspect of perceiving patterns, since the interrelationships among endemic taxa from such areas can provide testable hypotheses of biogeographic history.

In Central America, 10 major areas of herpetofaunal endemism are recognizable (Duellman, 1966; Savage, 1966; Müller, 1973) (Fig. 16):

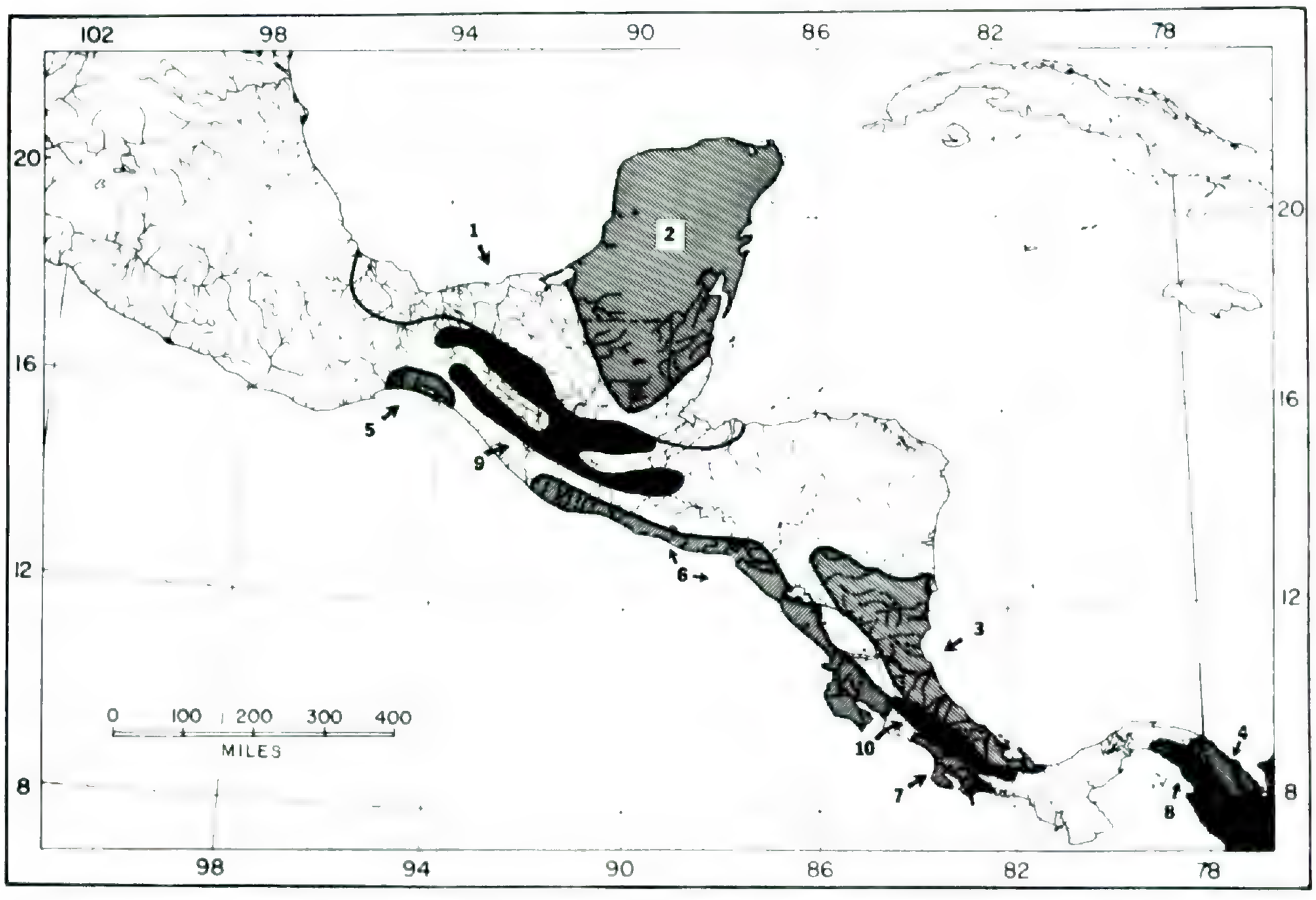


FIGURE 16. Principal Central American areas of herpetofaunal endemism; see text for description of numbered areas.

I. Lowland-Foothill Areas (0–±1,500 m).
   A. Atlantic Versant
      1. Northern—southeastern Mexico to western Honduras
      2. Yucatan—Yucatan Peninsula
      3. Southern—southern Nicaragua to northwestern Panama
      4. Chocoan—eastern Panama and Colombia
   B. Pacific Versant
      5. Tehuantepec—Plains of the Isthmus of Tehuantepec
      6. Southern—El Salvador to northwestern Costa Rica
      7. Golfo Dulcean—southwestern Costa Rica and adjacent Panama
      8. Savannas of eastern Panama

II. Highland Areas (1,500–).
      9. Nuclear—highlands of Chiapas, Mexico, Guatemala, El Salvador and Honduras
      10. Talamancan—highlands of Costa Rica and western Panama

As pointed out by Duellman (1966) and confirmed in the present analysis, the principal differences between lowland herpetofaunas in Central America involve east-west separation between Atlantic and Pacific areas. Along either coast, change in faunal composition is minimal in a northwest-southeast direction, except on the plains of Tehuantepec, the Yucatan Peninsula, around the Golfo Dulce, and in eastern Panama. The latter is empirically true, but only because eastern Panama contains wide-ranging forms from the Chocoan and northern South American areas of endemism.

The situation for the two highland areas is much different. They share few species in common and have a very high number of endemics. As will be seen below, they show considerable affinity to the endemic areas of the highlands of southern Mexico (Oaxaca and Guerrero) and these, in turn, are related to the Sierra Oriental and Occidental areas of endemism further northward in Mexico.

In either dispersal or vicariance theory, the areas of endemism represent isolates fragmented by vicariance events. Thus, these areas are presumed to have been isolated by physiographic or other environmental changes and tell us about the history of the region and its biota. Dispersalists tend to regard the endemic areas as milestones (or kilometer posts) along an old highway of dispersal that is now interrupted by barriers. The new super highways are more recent, ecologically fit corridors that are characterized by taxa in common or gradual changes in biotic composition along a gradient. Vicariists regard endemic areas as time capsules that contain data marking the timing of geologic and phylogenetic events. There is something to be said for both views. In many cases, disjunct areas of endemism on continental land masses appear to have been produced by an initial concordant dispersal, followed by a set of vicariance events that allowed for differentiation in isolation. The interrelations among areas of endemism may, thus, provide evidence for the timing and directionality of dispersal. Most vicariists (Rosen, 1976; Patterson, 1981) acknowledge that Central American generalized tracks represent two initial major dispersal events by two historical source units (a northern and a southern one) while claiming that concordant dispersal does not occur. On the other hand, much of the differentiation in any geographic region occurs *in situ* after an initial dispersal. In this sense, areas of endemism reflect vicariance events and form the units for evaluating interrelationships among areas. Recurrent concordance of biological and geological area-cladograms for these areas provides the basis for explaining causes of the patterns.

The matter of the interrelationships among areas of endemism in Central America will be discussed in another section. However, the following descriptive (phenetic) points need to be made:

* Each area, except 7, has endemic representatives of at least two tracks.

* North American-Central American and Middle American-Caribbean tracks have congruent endemism in areas 1, 2, 5, 6, 9.

* Middle American-Caribbean and South American-Caribbean tracks have congruent endemism in area 7.

* North American-Central American and South American-Caribbean tracks have congruent endemism in area 4.

* All three of these tracks have congruent endemism in areas 3 and 10.

To a very substantial degree, the generalized tracks and areas of endemism described above conform to patterns recognized in my earlier analysis. The generalized tracks appear to represent four historical source units whose constituent taxa have had an ancient and continuing association together. That association is reflected in the coincident distribution of diverse stocks of amphibians and reptiles along the tracks and coincident patterns of evolution that are correlated with major events in earth and environmental history. Genera and a few subgeneric groups whose distributions coincide with a particular track may be grouped together as a primary historical unit or Element. The four Elements recognized here correspond to the units discussed in my earlier papers (Savage, 1960, 1963,

TABLE 4. Component genera of principal historical units of the tropical Mesoamerican herpetofauna.

Old Northern (67)	Middle American (60)	South American (65)	Young Northern (7)
Salamanders: (9)	Caecilians: (2)	Caecilians: (2)	
Bolitoglossa A	*Dermophis*	*Caecilia*	
Bolitoglossa B	*Gymnopis*	*Oscaecilia*	
Chiropterotriton A			
Chiropterotriton B			
Lineatriton			
Oedipina			
Parvimolge			
Pseudoeurycea			
Thorius			
Frogs and Toads: (3)	Frogs and Toads: (14)	Frogs and Toads: (21)	
Rhinophrynus	*Gastrophryne*	*Protopipa*	
Scaphiopus	*Hypopachus*	*Chiasmocleis*	
Rana	*Bufo* (pt.)	*Relictivomer*	
Crepidophryne	*Glossostoma*		
Eleutherodactylus(pt.)	*Eleutherodactylus* (pt.)		
Hylactophryne	*Leptodactylus*		
Syrrhophus	*Physalaemus*		
Tomodactylus	*Pleurodema*		
Agalychnis	*Atelopus*		
Hyla (pt.)	*Bufo* (pt.)		
Plectrohyla	*Rhamphophryne*		
Pternohyla	*Dendrobates*		
Ptychohyla	*Phyllobates*		
Triprion	*Prostherapis*		
	Centrolenella		
	Anotheca		
	Gastrotheca		
	Hemiphractus		
	Hyla (pt.)		
	Phrynohyas		
	Phyllomedusa		

TABLE 4. Continued.

Old Northern (67)	Middle American (60)	South American (65)	Young Northern (7)
Turtles: (8)		Turtles: (1)	
Claudius		*Chelonoides*	
Kinosternon			
Staurotypus			
Dermatemys			
Chelydra			
Chrysemys			
Rhinoclemmys			
Terrapene			
Lizards: (14)	Lizards: (11)	Lizards: (16)	Lizards: (4)
Coleonyx	*Basiliscus*	*Anolis*	*Phrynosoma*
Lepidophyma	*Corytophanes*	*Enyalioides*	*Sceloporus*
Anelytropsis	*Ctenosaura*	*Morunasaurus*	*Urosaurus*
Eumeces	*Enyaliosaurus*	*Polychrus*	
Mabuya	*Iguana*	*Lepidoblepharis*	
Sphenomorphus	*Laemanctus*	*Phyllodactylus* (pt.)	
Abronia	*Norops*	*Thecadactylus*	
Celestus	*Phyllodactylus* (pt.)	*Ameiva*	*Cnemidophorus*
Coloptychon	*Gonatodes*	*Anadia*	
Gerrhonotus	*Sphaerodactylus*	*Bachia*	
Ophisaurus	*Aristelliger*	*Echinosaura*	
Heloderma		*Gymnophthalmus*	
Xenosaurus		*Leposoma*	
Bipes		*Neusticurus*	
		Ptychoglossus	
		Diploglossus	
Snakes: (33)	Snakes: (32)	Snakes: (24)	Snakes: (3)
Loxocemus	*Boa*	*Anomalepis*	*Leptotyphlops* (pt.)
Chironius	*Exiliboa*	*Helminthophis*	*Hypsiglena*
Coluber	*Ungaliophis*	*Liotyphlops*	*Crotalus*
Dendrophidion	*Adelphicos*	*Typhlops*	
Drymarchon	*Amastridium*	*Leptotyphlops* (pt.)	
Drymobius	*Atractus*	*Corallus*	
Elaphe	*Chersodromus*	*Epicrates*	

TABLE 4. Continued.

Old Northern (67)	Middle American (60)	South American (65)	Young Northern (7)
Ficimia	*Coniophanes*	*Trachyboa*	
Gyalopion	*Conophis*	*Clelia*	
Lampropeltis	*Crisantophis*	*Enulius*	
Leptodrymus	*Cryophis*	*Erythrolamprus*	
Leptophis	*Diaphorolepis*	*Leimadophis*	
Mastigodryas	*Dipsas*	*Lygophis*	
Nerodia	*Geagras*	*Manolepis*	
Oxybelis	*Geophis*	*Oxyrhopus*	
Pituophis	*Hydromorphus*	*Phimophis*	
Pseudoficimia	*Imantodes*	*Pseudoboa*	
Pseustes	*Leptodeira*	*Rhadinaea* (pt.)	
Rhinobothryum	*Ninia*	*Siphlophis*	
Rhinocheilus	*Nothopsis*	*Tripanurgos*	
Salvadora	*Pliocercus*	*Xenodon*	
Scaphiodontophis	*Rhadinaea* (pt.)	*Micrurus* (pt.)	
Sonora	*Rhadinophanes*	*Bothriopsis*	
Spilotes	*Scolecophis*	*Bothrops*	
Stenorrhina	*Sibon*		
Storeria	*Tantalophis*		
Symphimus	*Tretanorhinus*		
Sympholis	*Trimetopon*		
Tantilla	*Tropidodipsas*		
Tantillita	*Micrurus* (pt.)		
Thamnophis	*Agkistrodon*		
Toluca	*Bothriechis*		
Trimorphodon			
	Crocodilians: (1)	Crocodilians: (1)	
	Crocodylus	*Caiman*	

1966), but with substantial revision in content, based upon new findings on phylogenetic relationships, especially for snakes (Table 4).

Old Northern Element—derivative stocks of originally extratropical (subtropical-warm temperate) groups distributed more or less continuously and circumpolarly in early Tertiary, but forced southward and fragmented into several more or less disjunct components as a result of increased cooling and aridity trends and mountain building in late Cenozoic. This unit is comprised of taxa having long-term Laurasian affinities. Typical members of this element, including the "hanging" Middle American relicts, the frog family Rhinophrynidae, the turtle family Dermatemydidae, the lizard families Xantusiidae, Xenosauridae, and Helodermatidae, were widespread over much of North America to 40°N in early Tertiary. As I pointed out in 1966 and was confirmed by Rosen (1978), the Central American component of this stock has been disjunct from other components for most of later Tertiary and Quaternary time and has evolved *in situ* in Middle America.

South American Element—derivatives of a generalized tropical American biota that evolved *in situ* in isolation in South America during most of Cenozoic. The affinities of this unit are Gondwanian.

Middle American Element—derivative groups of a generalized tropical American biota isolated in tropical North and Central America during most of Cenozoic; developed *in situ* north of the Panamanian Portal and restricted by mountain building and climatic change in late Cenozoic to Middle America. Savage (1966) established the relationship of this unit to the South American Element and argued that a major vicariance event, the inundation of a putative Paleocene land bridge between Central and South America, led to their differentiation. Some workers believe groups placed here dispersed from South America across the proto-Antilles (Rosen, 1978) or the proto-Antilles and a later island archipelago, both located in the Panamanian Portal Zone (Duellman, 1979); subsequent differentiation has led to the distinctive aspects of this series of descendant groups.

Young Northern Element—derivatives from the generalized tropical American biota of early Tertiary that responded to the challenge of physiographic and climatic revolution in the middle latitudes of western North America and Mexico; essentially an *in situ* extratropical xeric derivative of the Middle American Element.

In my earlier discussion, I designated a number of subdivisions within the primary elements as "complexes." While these are still recognizable geographic patterns, since they correspond to components of a generalized track, they will be called components here. The most distinctive components of the tracks are represented by the nodes of endemic areas discussed above.

Development of the Herpetofauna

The principal contributions of vicariance theory to the field of historical biogeography do not come from the emphasis on vicariance events as primal modalities in shaping distribution patterns nor from the recognition that the patterns represent a trace on the earth's surface of ancient distributional events. Both of these ideas are part of conventional (dispersal) theory. Instead, it is the insistence

in vicariance theory on the search for general patterns and the rigorous testing of their generality that is distinctive. In the search for general pattern, vicariance biogeography proposes that the separate components of the pattern are historically linked to one another and to climatic, physiographic or tectonically induced changes in geography. A general pattern requires concordant dispersal and/or vicariance by many groups. Long-distance or random dispersal, by individual taxa, are stochastic events and are unlikely to produce general patterns. Nevertheless, distributional data alone rarely are sufficient to resolve the question of whether a particular general pattern has resulted from individual dispersal, concordant dispersal, and/or vicariance events. Instead, vicariance biogeography, in its latest formulation, initially seeks evidence, not as to the cause of the pattern, but as to whether the systematic relationships among related taxa in the geographic components of the pattern have a generality. The hypotheses of phylogenetic interrelationships among two or more taxa (each containing a minimum of three endemics) are transformed into one concerning interrelationships among areas. Comparisons with additional taxa test the hypothesis of area relations. The result is then compared for congruence with geologic and climatic history as a means to specify possible causes for the pattern in terms of a general explanation (Morse & White, 1979; and Fig. 7).

Application of this approach (Rosen, 1978) implies that the earth and life have evolved together, that paleogeographic and paleoclimatologic changes on the planet have produced the biological patterns, and that while most of the observed patterns will be specified by events in earth history, some (individual dispersals) will not. It further implies that a knowledge of the evolutionary relationships among taxa will allow for prediction of previously undetected events in earth history. Conversely, a knowledge of earth history must provide a basis for predicting the interrelationships among taxa, a point not mentioned by the vicariists, but implicit in their argument. We will return to this latter point below.

ALTERNATIVE HYPOTHESES

At the present time there are three conflicting theoretical explanations of the biogeography of the Central American herpetofauna (Savage, 1966; Rosen, 1976; Duellman, 1979). Each of these explanations shows some correlation with ideas on the distribution of other groups of organisms in the region (i.e. plants, freshwater fishes, and mammals), so that there appears to be several repetitive general patterns. Presumably, the best explanation of the history of amphibians and reptiles in Central America should provide a basis for explaining the pattern shown in other groups as well.

In the following paragraphs, I will briefly outline the major features of each distributional theory; review each theory in the light of the revised data set, generalized track analysis, and historical source unit assignment provided in the present paper; propose a revised theory to explain the herpetofaunal pattern; and compare these results to patterns for other groups.

The essential features of the three principal theories proposed to explain the origin and history of the Central American herpetofauna are summarized below (Figs. 2–5):

1. Savage (1966)—a major vicariance event in early Tertiary, the inundation of the original Isthmian Link, fragmented an ancestral tropical American herpetofauna into two isolated elements, one in Middle America and one in South America, that underwent differentiation *in situ* for most of the remainder of the Tertiary. A second vicariance event associated with mountain building and climatic changes from Eocene onward led to the isolation of a number of stocks of northern affinities (the Central American component) in Mesoamerica, where they underwent *in situ* differentiation in association with Middle American groups of southern affinities. Upon re-establishment of the Isthmian Link in Pliocene, some South American groups dispersed northward and some stock of the autochthonous Middle American element and associated, originally, northern taxa dispersed southward, to obscure the formerly complete distinction between Mesoamerican and South American herpetofaunas.

2. Rosen (1976)—a major vicariance event in early Tertiary caused by the eastward drift of the proto-Antilles from their position between Nuclear Central America and South America fragmented a formerly more or less continuous biota to isolate Middle American, Antillean, and South American components. The same process fragmented a northern unit of the biota into Middle American and Antillean components. Subsequent mountain building and climatic change in the region of northern Mexico essentially isolated both northern and southern elements in Middle America from Eocene to Pliocene (Axelrod, 1975; Rosen, 1978). Establishment of the Isthmian Link in Pliocene led to limited dispersal between Central and South America, in both directions.

3. Duellman (1979)—island-hopping dispersal events involving the proto-Antilles in early Tertiary and a later Middle American archipelago allowed a number of familial level groups (13–14) to immigrate from South America to Central America and vice versa (4–6). On establishment of the Isthmian Link, in Pliocene, many additional groups dispersed in both directions.

A fourth alternative, not seriously proposed by anyone, might be to attribute the current patterns of distribution in Central America to a primarily post-Miocene dispersal of South American groups into the region, with subsequent rapid differentiation in endemic Middle American taxa.

As may be seen from this summary, the primary differences among the conflicting theories center on the nature of biotic relations, geologic events, and dispersals involving South America and Nuclear Central America. The interpretations of Savage and Rosen, relative to the incorporation of a northern component into the biota of Middle America, due to mountain building and climatic change, that isolated these groups from their allies in eastern North America by Oligocene, are essentially similar. While Duellman does not address this matter directly, since his concern is principally with Central and South American interrelationships, he (p. 16) appears to concur with my 1966 views. Other subsidiary problems involve the composition and time of arrival of northern groups in Central America, the differentiation of lowland areas of endemism, and the origin of montane isolates. Each of these problem areas will be addressed below.

Ideally, the best way to proceed in the analyses of alternative hypotheses would be to employ the method of Morse and White (1979) to discern if there are repetitive patterns of phylogenetic relationships that can be transformed into

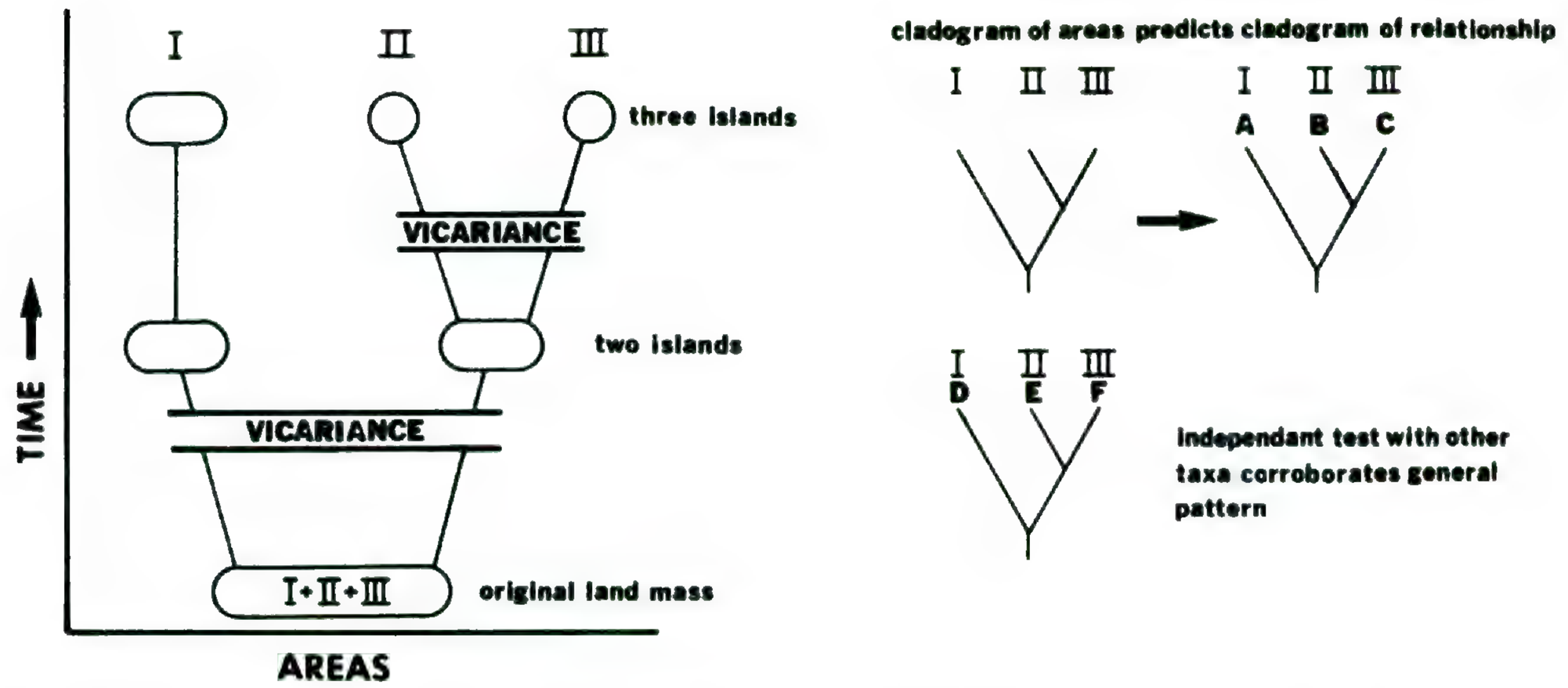


FIGURE 17. Prediction and testing of phylograms from area cladogram based on known geologic history.

general patterns of area relationships. These could then be compared with alternate theories, to test congruence between phylogeny and geography. Unfortunately, the constraints of the cladistic-vicariistic analytical method make this alternative unfeasible in application, first, because there are not a sufficient number of cladistic analyses available for the study area. For this reason, it is not possible to posit sequences of geography events based upon the branching sequences of area cladograms constructed. If one accepts the underlying concept of this approach, i.e. that earth and life have evolved together, and that general patterns of biotic distributions reflect earth history, another method may be used to estimate or test the validity of a biogeographic hypothesis. This method simply reverses the procedure of area-cladogram construction to use events in earth history to predict general recurrent patterns of phylogenetic relationship. Obviously, this approach implies a reciprocal relationship between earth history and the history of life and means that the statement:

pattern of paleogeographic and paleoclimatic change → phylogenetic change,

may be read from either direction. Thus, if we know something about patterns of earth history, it is possible to predict hypothetical phylogenetic patterns that can be tested against actual patterns. For example, if we know in some detail the history of a region which has been fragmented by a pair of vicariance events at known times, we should be able to predict three taxa—three area cladograms of relationships that can then be tested by actual phylogenetic analyses (Fig. 17). In areas for which geologic history is well known, this method provides interesting promise.

Unfortunately, the Central American region is among the most geologically complicated and controversial regions in the world. It remains impossible to obtain the necessary consensus of geologic opinion that would allow construction of a cladistic statement of geologic history, especially as it affects the Nuclear Central American-South American interconnection. The cladistic-vicariist method does, however, offer another way to attack the problem in many cases. This

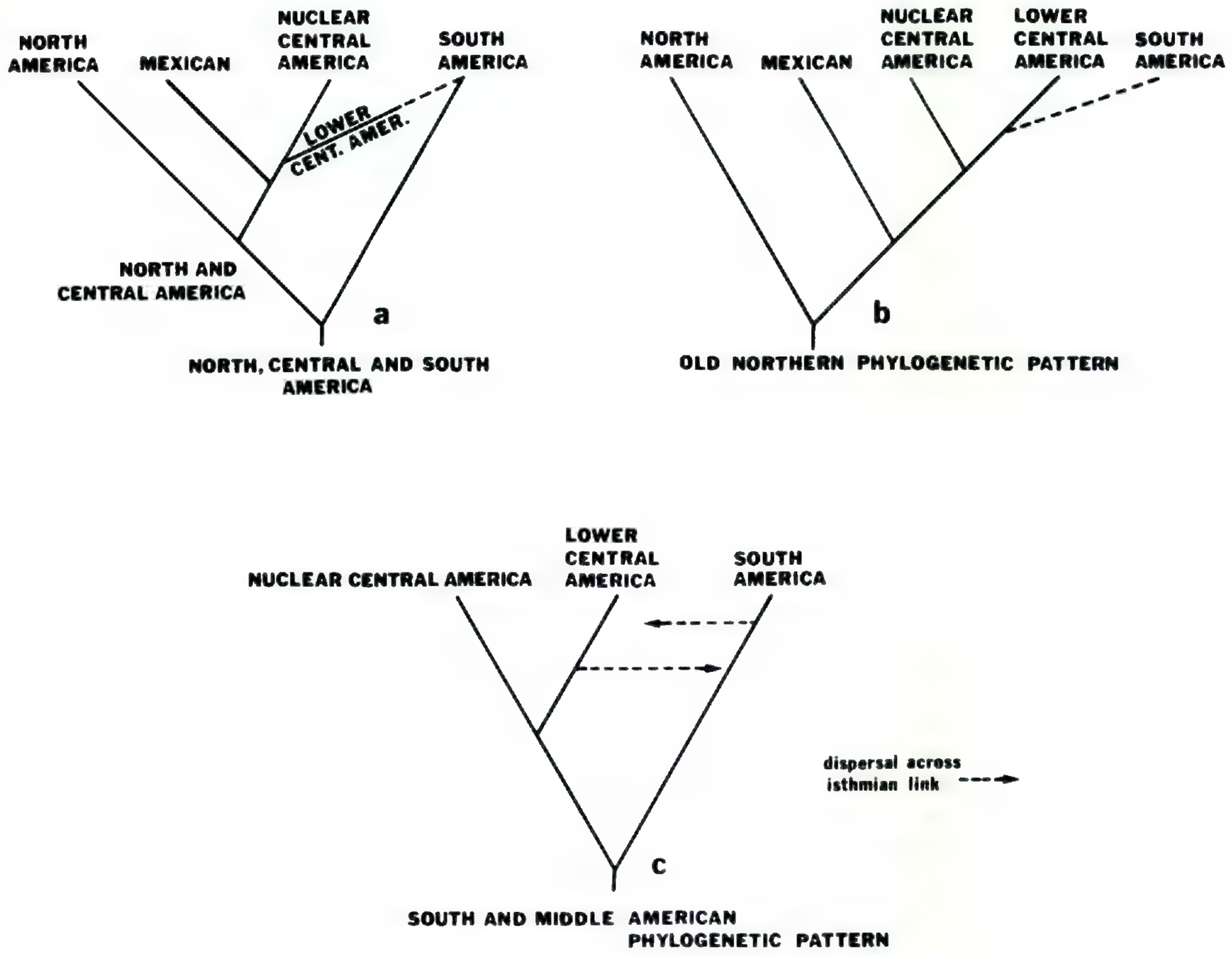


FIGURE 18. Cladogram of areas for the Americas based upon known geologic events (a). Predicted phylograms for major historical units of the herpetofauna, Old Northern (b), and South and Middle American (c).

is simply to transform the key elements of a biogeographic theory into a general cladogram of areas and use it to predict a general pattern of phylogenetic relationships. This hypothesis of pattern may then be tested by cladistic analysis of actual patterns for different taxa. Repeated congruence of relationship could then be interpreted as corroborating the theory. Substantial discongruence will suggest that aspects of the proposed theory are incorrect. Modifications of the theory may then be tested against the biological cladograms. In essence, this is what Rosen (1976) did when he constructed a model of Caribbean geological history (Pregill, 1981) and predicted phylogenetic patterns for northern and southern elements of the biota of Central America, the Antilles, and South America (Fig. 5).

In the present instance, I attempted to utilize the same method to distinguish among the several alternate hypotheses of Central American biogeography. It was thought that the several hypotheses would contain unique aspects that, when reduced to hypothetical area cladograms, would predict differences for phylogenetic pattern. This is not the case. All three hypotheses predict the same phylogenetic patterns (Fig. 18) as related to Central America. The reason again lies in the complex and unique history of the region, which forms a zone of mixing between two formerly isolated biotas now in contact over an emergent land connection, and the fact that all three views agree that Nuclear Central America

clearly was populated by a whole host of groups from South America in the distant past and remained isolated from South America for millions of years. In other words, the three hypotheses predict the same phylogenetic patterns; they disagree as to process.

The Duellman model involves multiple, independent, long-distance dispersals by individual taxa across the Panamanian portal at different times during Tertiary, but primarily, in the direction from South to Central America. Since this view requires an individual explanation for each taxon involved, no general pattern can be expected to emerge. The model is further complicated by Duellman's estimate of 18–20 dispersals southward and 23–25 northward, across the Isthmian Link. As pointed out by the vicariists, dispersal theories such as this are difficult to test. Since dispersal is invoked *a priori* as an explanation, each complication in interpretation is explained by another individual dispersal event, and no real decision can be made that parsimoniously minimizes the number of separate assumptions entailed in the explanation. Any parsimony decision only becomes possible when distribution patterns can be shown to have some significant generality, i.e. they occur in a number of different monophyletic groups. These factors mitigate against or make impossible testing of most theories of this kind. For this reason, theories of this kind may be called special dispersal theories since each dispersal is a unique event. Three features usually characterize long-distance dispersal by individual taxa when the presumed dispersed taxa are grouped as a unit: 1) they constitute a relatively small proportion of their respective biotas; 2) they appear to be a relatively random sample of groups from the presumed source area; and 3) they do not fit a general pattern of concordant distribution.

With these points in mind, let us review Duellman's theory of Central and South American relationships for south to north overwater dispersals prior to the Pliocene. Included groups are: ancestors of Central American Caeciliidae, *Eleutherodactylus, Agalychnis,* Hylidae, Microhylidae, Gekkonidae, primitive Iguanidae, anolines (Iguanidae), Teiidae, Leptotyphlopidae, Typhlopidae, Colubridae (Xenodontinae), and Micruridae (?). These groups comprise an important component in the Middle American herpetofauna; they are a major sample of South American stocks and they conform to the generalized track, congruent with that of other Middle American unit groups. In most cases, they are the endemic sister taxa of endemic South American groups as well. There seems no reason to regard any of these groups as special cases of dispersal, since they conform to the general pattern of vicariance discussed below.

Similarly, while not an issue here, the presumed north to south overwater dispersers identified by Duellman seem to conform to general patterns and do not seem to require special dispersals; they include: Testudinidae, iguanines (Iguanidae), Anguidae, Crocodylidae and, questionably, Colubridae and Viperidae (Table 4). Both the Savage (1966) and Rosen (1976) theories for the biogeography of the region depend upon major vicariance events, although I emphasized then more than I would now, aspects of Plio-Pleistocene dispersals to explain some features of the distribution patterns. Both emphasize 1) an ancient (Cretaceous-Paleocene) major concordant dispersal of southern stocks into Central America; 2) subsequent isolation of the two stocks by a major vicariance event,

the formation of the Panamanian portal region; 3) differentiation *in situ* both north and south of the portal to produce the distinctive components that now are sympatric in the Isthmian region; 4) association of a series of northern groups with the Middle American component during much of Cenozoic; 5) isolation of Middle American and their northern associates (the Central American component) from the areas occupied by the latter's cognates in eastern North America, through the impact of the vicariance events of mountain building and climatic compression, from Oligocene onward.

Based upon my earlier study and the re-analysis undertaken here, I wish to point out those areas of the Rosen (1976) dispersal-vicariance model that do not fit the herpetological data. It should be noted as well, that although Rosen (pp. 445–446) inveighs against the concept of concordant dispersal, he, of course, evokes it to explain (p. 453) the invasion of Nuclear Central America by northern and southern groups. Clearly, his vicariance theory (and all others), is based upon initial concordant dispersal of many groups, followed by fragmentation. When the geographic source of the original concordant dispersal is identified, even in such broad terms as Gondwanian or Southern, as in Rosen's study, the vicariists are, in effect, using the much despised (Croizat et al.) center of origin concept in theory construction. Directionality of the concordant dispersals, one from the north and one from the south, forms an essential ingredient in Rosen's vicariance theory.

Rosen's theory was developed primarily to explain Caribbean biogeographic patterns. For this reason, he did not fully treat nor consider the Pacific lowlands and highlands of Central America in his account. In addition, one of his major focuses was on the relationships of the Antillean biota with reference to other American land masses. Partially, for these reasons, Rosen did not emphasize the marked distinctiveness in group distributions and relationships for the taxa subsumed in his South American-Caribbean track, which have led me to distinguish South and Middle American Elements. Failure to do so is a reflection of the inability of vicariance theory to sort out relatively recent dispersal events in which, as in this case, a major distributional barrier (the marine portal) has been removed. A review of the taxa lying on Rosen's South American-Caribbean track shows that many of those now found in Central America represent Pliocene to Recent dispersal across the Isthmian Link. This pattern overlays the ancient track produced by concordant dispersal prior to the complete separation of Central and South American biota much earlier in Tertiary. For this reason, I prefer to emphasize the autochthonous Middle American and South American tracks as distinct units, in order to reduce the contamination by relatively recent dispersal from south to north and vice versa that tend to obscure the general pattern produced by the major vicariance event.

Finally, I find no evidence that would support the idea that northern taxa (Old Northern Element) were in Nuclear Central America in substantial numbers during Cretaceous, when, according to Rosen's model, they dispersed southward onto the proto-Antilles (Fig. 5). Indeed, one wonders why, if northern taxa were present, did they not have a major dispersal across the proto-Antilles southward? This is especially puzzling, if one accepts Rosen's idea that at the same time

southern groups dispersed northward across the proto-Antilles. As will be pointed out below, a number of Middle American Element taxa were included with his northern (North American-Caribbean) track to inadvertently confuse this issue. These stocks are clearly of southern relations.

Recently, Pregill (1981), utilizing the geological data of Perfit and Heezen (1978), and a dispersalist approach to explaining recent and fossil vertebrate distributions in the Antilles, severely criticized Rosen's model. This eventuality was predicted by Patterson (1981), as noted in an earlier section of the present paper. The key element in Pregill's exposition is the conclusion that there were no proto-Antilles in the Panamanian portal region at any time and that the Greater and Lesser Antilles have had an entirely different history from that proposed by Rosen and from one another. While it is difficult to select from among the several geological models proposed for the Antilles, since Rosen's paper appeared (Owen, 1976; Carey, 1976; Shields, 1979; Lillegraven et al., 1979; Melville, 1981), not all of these support Pregill's contention that the Antilles are essentially oceanic islands populated by overwater dispersal. In any event, I join Patterson (1981) in concluding that the new discoveries in Caribbean geology in no way falsify Rosen's empirical evidence, which still demands explanation. Review of that evidence (Table 5 and Figs. 12–15) indicates that the herpetofauna of the Antilles consists of Old Northern, Middle American, and South American Elements. The former two tend to be concentrated in the Greater Antilles, especially on Cuba, and the latter in the Lesser Antilles. How these patterns may have come to be formed, whether by dispersal or vicariance, will be returned to below.

A REVISED MODEL OF HERPETOFAUNAL HISTORY

My revised model is essentially a vicariance one. It recognizes the concepts of concordant dispersal, historical source unit, and area of origin (concepts that arch-vicariists may decry) as useful devices for biogeographic theory construction. It emphasizes the relationship between these concepts and the evidence of congruent distribution patterns as seen in generalized and component tracks. It accepts the notion that the model's validity will be tested by cladistic analysis of interrelationships transformed to area cladograms and by new findings in paleogeography and paleoclimatology.

The essential framework of the model differs in no great way from that proposed 15 years ago, and the summary given below will not be detailed.

All evidence points to an ancient contiguity and essential similarity of a generalized tropical herpetofauna that ranged over tropical North, Middle, and most of South America in Cretaceous-Paleocene times. Descendants of this fauna are represented today by the South and Middle American tracks (Elements). To the north of this fauna ranged a subtropical-temperate Laurasian derived unit, today represented by the Old Northern Element (track). By Eocene, northern and southern fragments of the generalized tropical units had become isolated in Middle and South America, respectively. Differentiation *in situ* until Pliocene produced the distinctive herpetofaunas that became intermixed with the establishment of the Isthmian Link (Fig. 2).

By Eocene a substantial number of Old Northern groups became associated

TABLE 5. Distribution of the genera of amphibians and reptiles on major island groups.

	Greater Antilles				Lesser Antilles	Galapagos
Bufonidae:						
Peltophryne	C	H	PR			
Hylidae:						
Calyptahyla	J					
Hyla	H	J			*Hyla*	
Osteopilus	C	H	J			
Leptodactylidae:						
Eleutherodactylus	C	H	J	PR	*Eleutherodactylus*	
Leptodactylus	H	PR			*Leptodactylus*	
Sminthillus	C					
Emydidae:						
Chrysemys	C	H	J	PR		
Testudinidae:						
Chelonoides	C*				*Chelonoides**	*Chelonoides*
*Monochelys***						
Iguanidae:						
Anolis	C	H	PR		*Anolis*	
Chamaeleolis	C					
Chamaelinorops	H					
Cyclura	C	H	J	PR*	*Cyclura*	*Amblyrhynchus*
					Iguana	*Conolopus*
Leiocephalus	C	H	J	PR*	*Leiocephalus*	*Tropidurus*
Norops	C	J				
Gekkonidae:						
Aristelliger	H	J				
Gonatodes	C	H	J			
Hemidactylus	C	H	PR		*Hemidactylus*	
Phyllodactylus	H	PR			*Phyllodactylus*	*Phyllodactylus*
Sphaerodactylus	C	H	J	PR	*Sphaerodactylus*	
Tarentola	C				*Thecadactylus*	
Gymnophthalmidae:					*Bachia*	
					Gymnophthalmus	
Teiidae:						
Ameiva	C	H	J	PR	*Ameiva*	
					Kentropyx	
Scincidae:						
Mabuya	H	J	PR		*Mabuya*	
Xantusiidae:						
Cricosaura	C					
Anguidae:						
Celestus	H	J				
Diploglossus	C	H	PR		*Diploglossus*	
Sauresia	H					
Wetmorea	H					
Amphisbaenidae:						
Amphisbaena	C	H	PR		*Amphisbaena*	
Cadea	C					
Typhlopidae:						
Typhlops	C	H	J	PR	*Typhlops*	

TABLE 5. Continued.

Greater Antilles					Lesser Antilles	Galapagos
Leptotyphlopidae:						
Leptotyphlops	H				*Leptotyphlops*	
Boidae:						
					Boa	
					Corallus	
Epicrates	C	H	J	PR	*Epicrates*	
Tropidophiidae:						
Tropidophis	C	H	J			
Colubridae:						
Alsophis	C	H	J	PR	*Alsophis*	
Antillophis	C	H				
Arrhyton	C	J	PR		*Arrhyton*	
					Chironius	
Darlingtonia	H				*Clelia*	
Hypsirhynchus	H				*Dromicus*	*Dromicus*
Ialtris	H				*Mastigodryas*	
Nerodia	C				*Pseudoboa*	
Tretanorhinus	C					
Uromacer	H					
Viperidae:						
					Bothrops	
Crocodylidae:						
Crocodylus	C	H	J		*Crocodylus*	

C = Cuba.
H = Hispaniola.
J = Jamaica.
PR = Puerto Rico.

* Fossil.
** Fossil on Mona Island between Jamaica and Puerto Rico.

with Middle American stocks in Mexico. As the former continuity between that region and what is now the eastern United States was affected by mountain building and subsequent (Oligocene-Pliocene) climatic change, these components became disjunct (Axelrod, 1975). This disjunction (Rosen, 1978) allowed differentiation of what I have continued to call the Central American Component of the Old Northern Element, which evolved in association with the Middle American Element for the remainder of Cenozoic. Thus, the initial organization of what was to become the Meso-American herpetofauna involved a pair of vicariance events: 1) complete geographic isolation from South America and 2) fragmentation and isolation of the Central American Component from its northern congeners, by a combination of physiographic and climatic factors. By Oligocene, most of the genera or their ancestors, which now form the Old Northern and Middle American Elements (Table 4), were present in the region.

A major physiographic development, the uplift of the main mountain axis of Mexico and Central America, created two important additional vicariance events. This process seems to have had a north to south sequence, with the Sierra Madres of Mexico present as upland areas in Oligocene, and the highlands of Nuclear Central America developing in Miocene. The final sequence of uplift was in lower Central America leading to the closure of the Panamanian Portal in Pliocene. A

primary vicariance effect of the uplift was to gradually fragment what was a rather homogeneous Mesoamerican herpetofauna into three groups: a) an eastern lowland, b) a western lowland, and c) an upland assemblage. Although I previously emphasized climatic differences between eastern (humid, evergreen forests) and western lowland (subhumid-semiarid, deciduous, and thorn forests) areas to explain the two lowland patterns of distribution, it now seems that the important phylogenetic factor (progenetic) was the vicariance effect of mountain building. As pointed out, many species and most genera of lowland groups in Central America are found on both Pacific and Caribbean coastal strips. Duellman (1966) and I have also pointed out the relative homogeneity of the herpetofauna on each lowland versant, with most genera and species widely distributed. Examples suggesting the effect of this vicariance event include (Figs. 19–20):

A. Endemic Genera

Atlantic	Pacific
*Gymnopis**	*Loxocemus*
Anotheca	*Crisantophis*
	Leptodrymus
	Scolecophis

B. Endemic Genera With Endemic Species on Both Versants

Triprion
Basiliscus
Enyaliosaurus
Symphimus

C. Species Pairs

Atlantic	Pacific
Bufo valliceps	*Bufo luetkenii*
Dendrobates pumilio	*Dendrobates granuliferus*
Phyllobates lugubris	*Phyllobates vittatus*
*Hyla microcephala**	*Hyla robertmertensi*
Eumeces schwartzei	*Eumeces managuae*
Rhinoclemmys annulata	*Rhinoclemmys pulcherrima*
Bothriechis annectans	*Bothriechis ophryomegas*

* On Pacific versant in lower Central America.

As the mountains were uplifted, the distributions of certain other groups, perhaps originally associated with the low uplands of earlier times, became fragmented onto the three major highland areas today comprising the backbone of Middle America. This fragmentation has led to the development of endemic montane isolates from ancestors with a formerly continuous north to south range. I previously had considered dispersal from one highland to the other as a significant factor responsible for distributions corresponding to this pattern among the several salamander lines; in several groups of montane tree-frogs (Fig. 21); a number of lizards: *Norops*, *Sceloporus*, and *Gerrhonotus* (Figs. 22–23); and some snakes

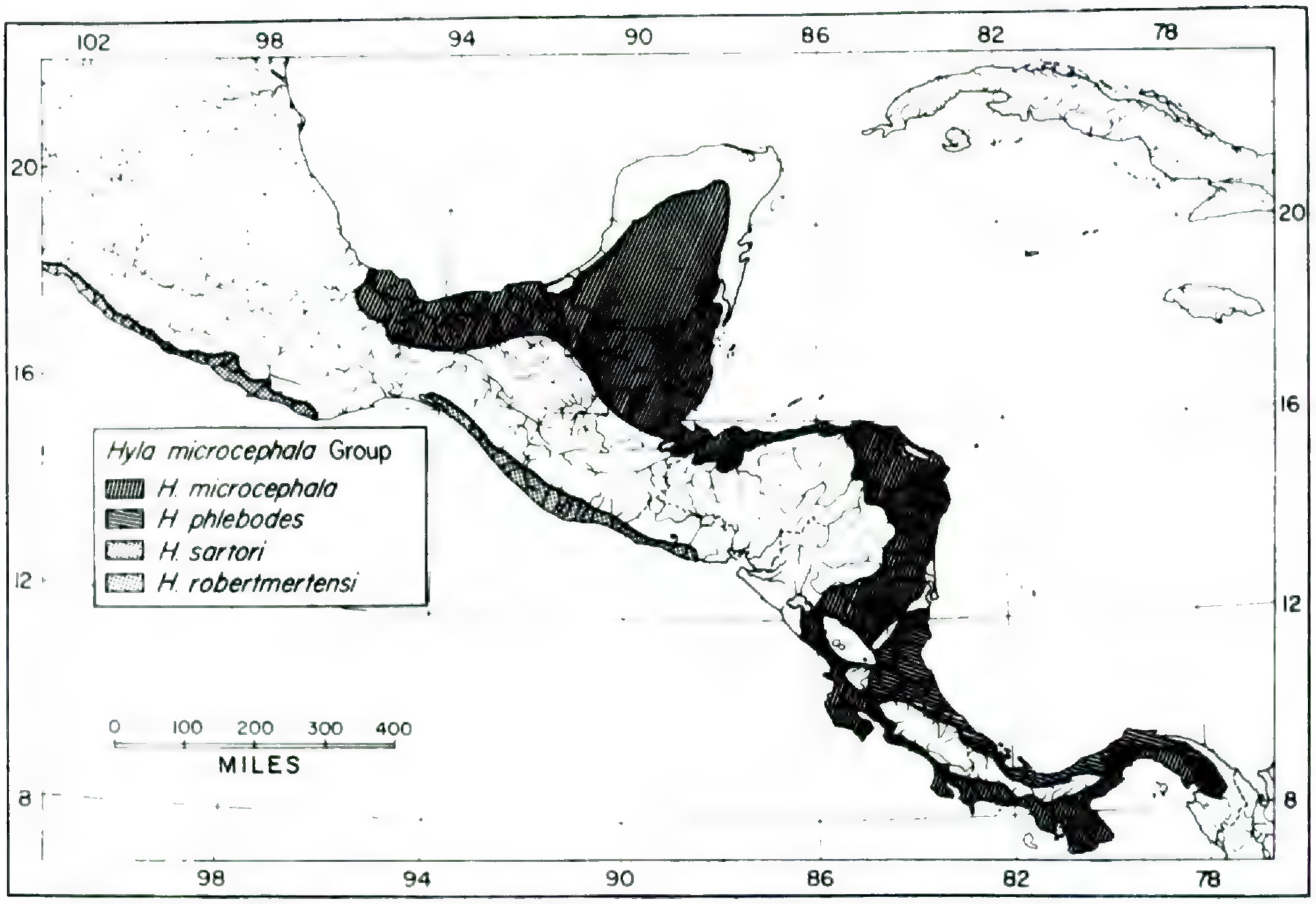


FIGURE 19. Distribution of tree-frogs of the *Hyla microcephala* stocks, showing Atlantic-Pacific fragmentation produced by uplift of the main mountain axis of Mexico and Central America.

of the genera *Geophis, Ninia, Rhadinaea,* and *Bothriechis*. I now believe that the distinctive montane herpetofaunas of the southern Sierras of Mexico, Nuclear Central America, and the Talamanca area developed more or less *in situ* from ancestors that "rode" the uplifted areas and evolved with them. Each endemic montane area then represents an uplifted island biota vicariated from a more or less similar sea of widely distributed ancestors.

This conclusion was anticipated in my 1966 account (p. 763), where I pointed out the striking differences among the herpetofaunas of the highlands of southern Mexico, Guatemala, and the Talamanca region. As noted then, "It must be stated emphatically that both the northern and southern highland areas of Central America have indigenous faunas drawn, for the most part, from mesic lowland ancestors in the two regions and differing, strikingly, from one another in almost every facet of herpetofaunal composition."

The minor role of Young Northern Element groups in Central America was emphasized in my previous paper and with the discovery that many genera previously included with this unit belong with the Old Northern component (Table 4), that role is even further reduced. Only the lizard genera *Sceloporus* and *Cnemidophorus* and the snake genus *Crotalus* (Table 4) contribute to the region. *Cnemidophorus* and *Crotalus*, and a number of *Sceloporus*, are generally associated with dry formations. One group of *Sceloporus* is montane in distribution, suggesting that the ancestor of this stock was widely spread over the lowlands and fragmented into isolates by riding the emergent separate highlands (Fig. 22).

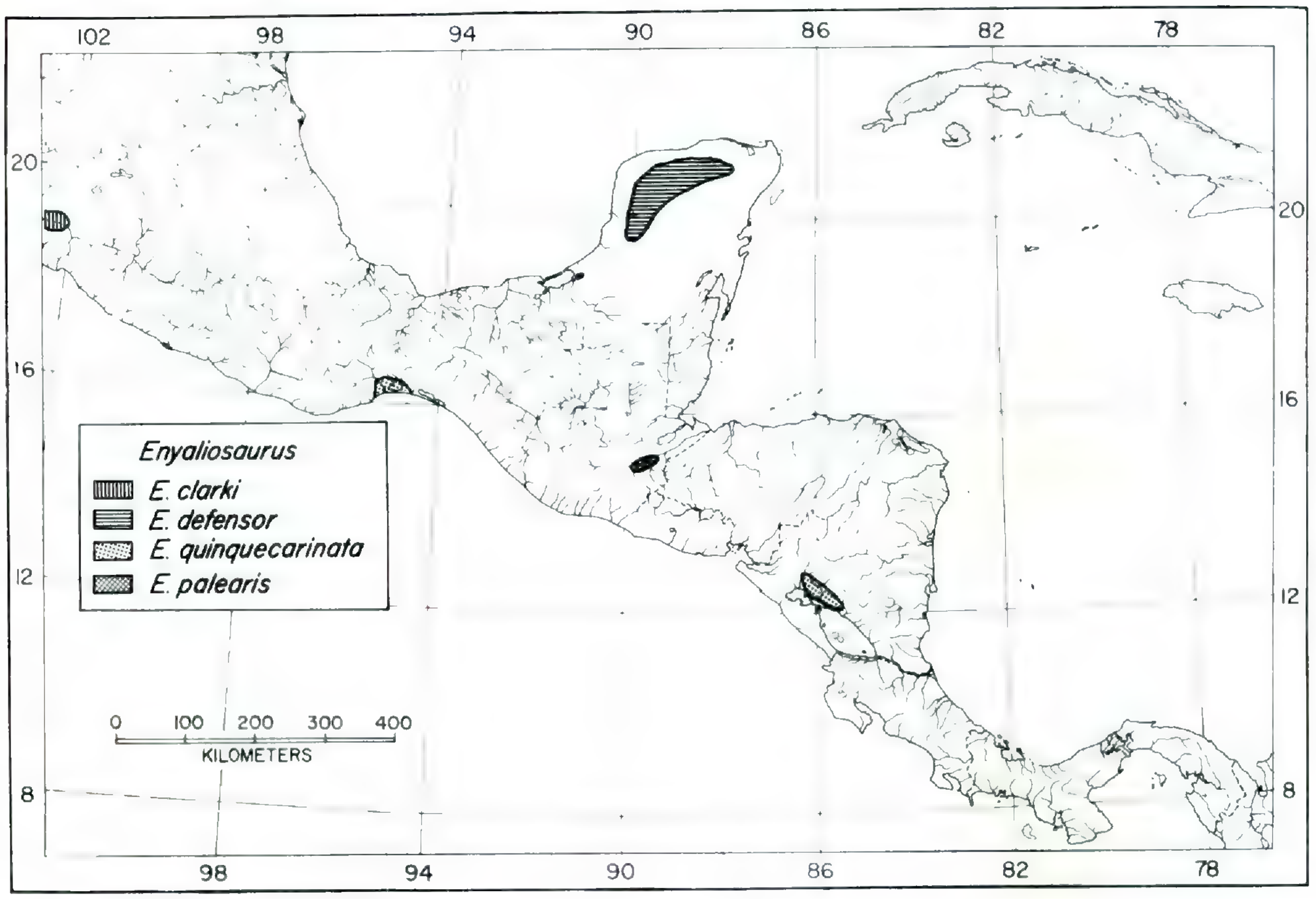


FIGURE 20. Distribution of the iguanid lizard genus *Enyaliosaurus*, illustrative of the fragmentation of lowland groups into Atlantic and Pacific components by the uplift of the main mountain axis of Mexico and Central America.

The final major factor in shaping the herpetofauna of Central America was the complete emergence of the Panamanian Isthmus in Pliocene to directly connect North and South America. While there remains some question as to whether the connection was completed in early Pliocene (Savage, 1974; Raven & Axelrod, 1974) or late Pliocene (Webb, 1977; Marshall et al., 1979), a difference between 5.7 or 3 m.y. B.P., respectively, the exact dating does not affect our story. The reconnection led to the dispersal of many South American Element genera northward and permitted immigration by some Old Northern and many Middle American stocks into South America. These concordant dispersal events, also well documented for other major groups and fully confirmed by the mammal fossil record (Marshall et al., 1979), conclusively demonstrate that dispersal of this kind cannot be discounted in biogeographic theory as vicariists attempt to do. In any event, 64 living generic level taxa of clearly South American origin have dispersed across the Isthmus to contribute to the Central American herpetofauna (Figs. 2, 13). Most of these groups are restricted to the region from eastern Panama to Costa Rica, so that the South American influence is minimal over most of Mesoamerica. Similarly, the greatest number of Middle American generic level taxa and species is found in northwestern South America.

The recent herpetofaunas of Central America, except those in eastern Panama, are based upon a fundamental core of autochthonous Middle American groups whose history in the region goes back at least to early Tertiary. Coexisting with

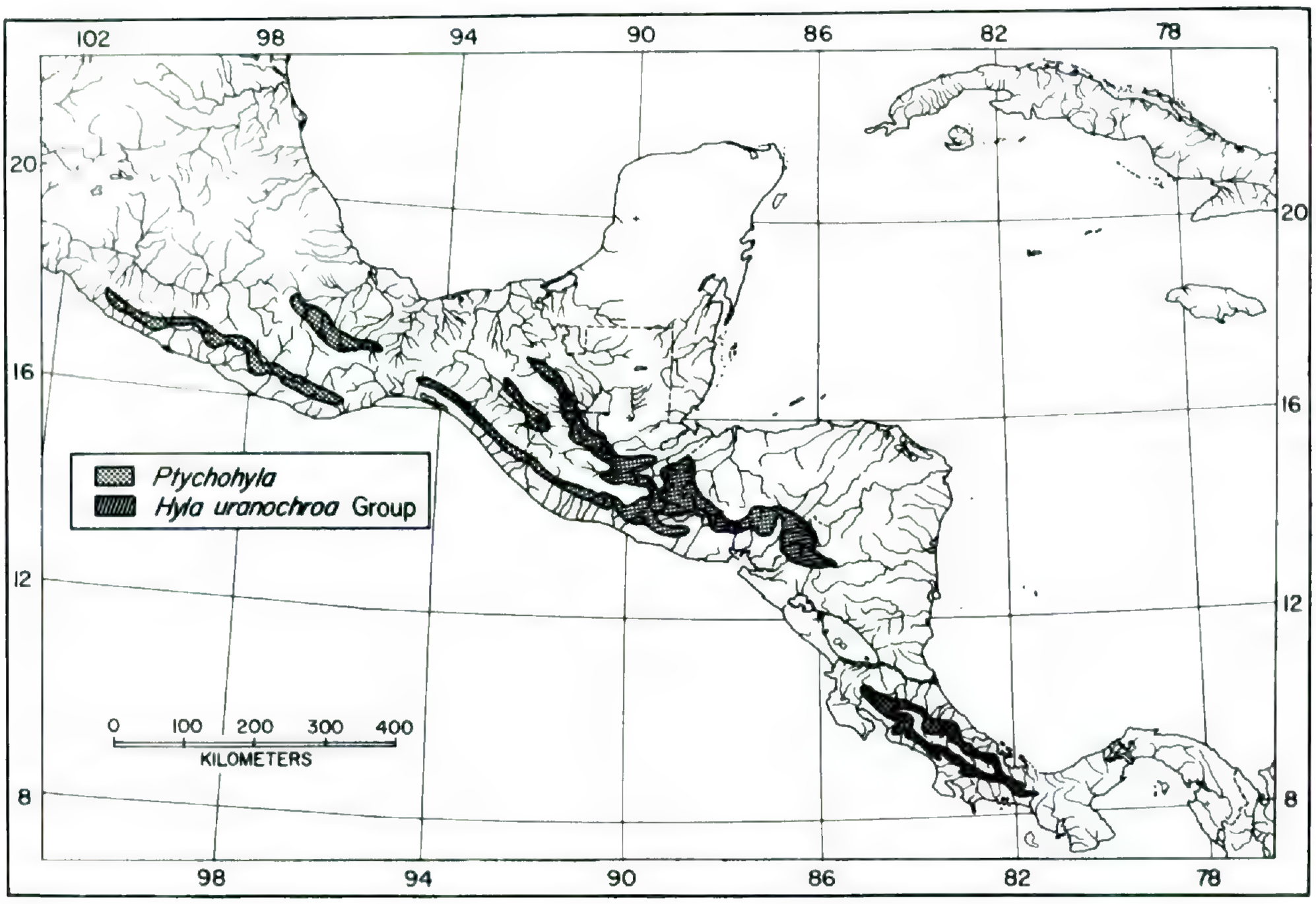


FIGURE 21. Distribution of the tree-frogs of the genus *Ptychohyla* and *Hyla uranochroa* group, showing the fragmentation of once continuous ranges by the gradual uplift of the Mesoamerican montane regions.

this unit throughout the region are a series of autochthonous derivative stocks of Old Northern relationships that have been in the region from Eocene-Oligocene times onward.

Uplift of the highland regions of Mexico, Nuclear Central America, and the Talamanca region carried with them groups of mesic lowland derivation from both Middle and Northern units. These stocks have produced minor evolutionary radiations in the two Central American highland zones, which differ markedly from one another and the Sierras of Mexico. The impact of this process of mountain building fragmented the lowland herpetofauna into eastern and western components as well. The effects of climatic changes toward more xeric conditions along the Pacific coastal lowlands from Pliocene onward seem to have sorted out a relatively small number of taxa from an originally more diverse fauna. The highland and western lowland herpetofaunas include a representation of Young Northern groups, which may also occur in subhumid to xeric situations on the Atlantic versant, but this component is relatively insignificant. In Panama and Costa Rica, particularly, South American Element taxa contribute significantly to the fauna and predominate in eastern Panama.

DISTRIBUTIONAL EVIDENCE FROM OTHER MAJOR GROUPS

The most interesting aspects of the model outlined in the preceding section remain: 1) the distinction by some kind of vicariance event of the Middle Amer-

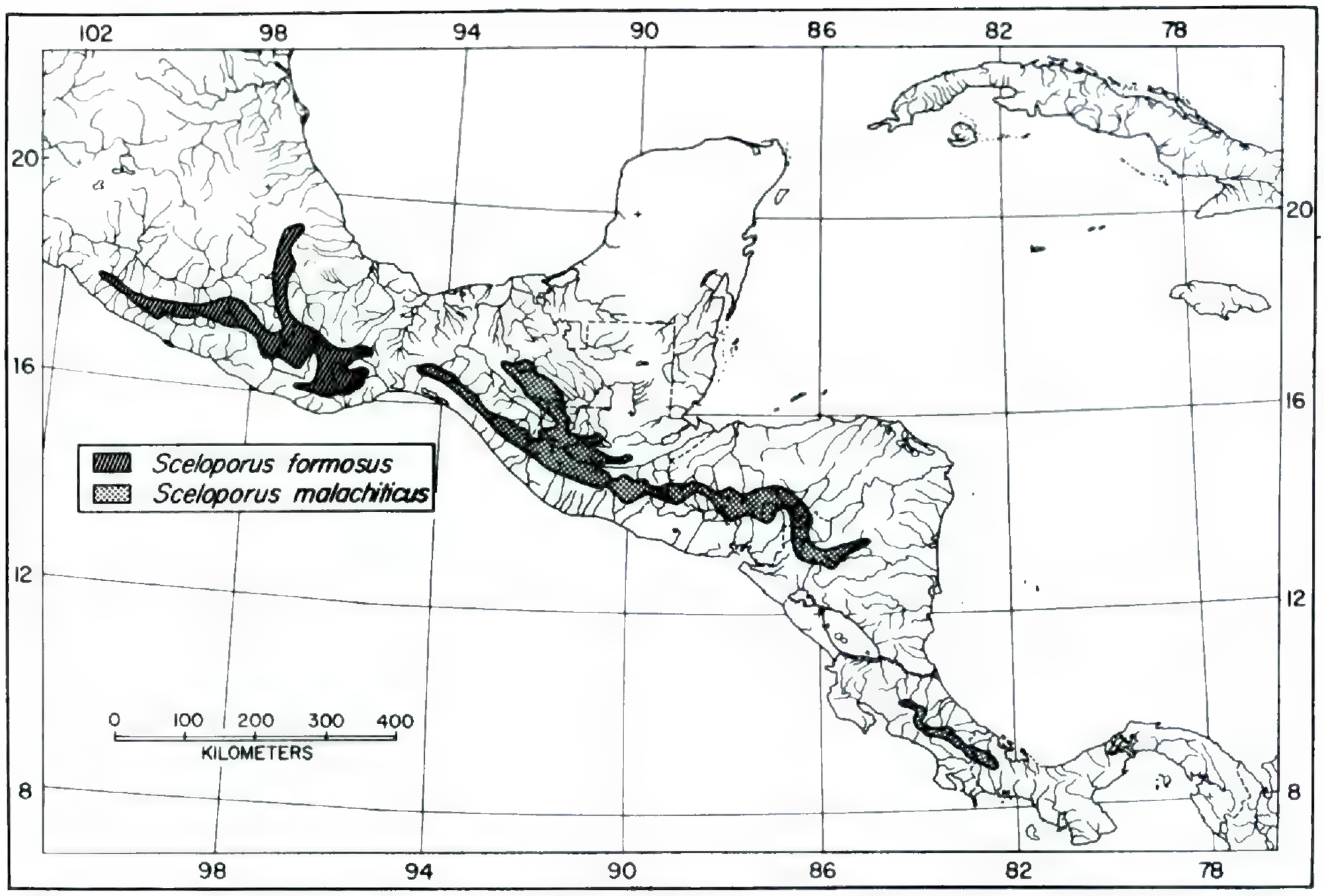


FIGURE 22. Distribution of the spiny lizard of the *Sceloporus formosus* group, illustrating fragmentation by uplift of the Mesoamerican montane regions.

ican and South American source units prior to Eocene time and, 2) the coexistence of co-differentiation of disjunct Old Northern (Central American Component) taxa along with the Middle American stocks. The question that I will attempt to answer here is: Do other major groups of organisms show similar patterns of distribution and relationships? An answer of "yes" would corroborate the herpetofaunal model as having generality. An answer of "no" would require modification or rejection of the concept.

Raven and Axelrod (1974) presented a strongly dispersalist interpretation of the relationship of South and Central American angiosperms. Their conclusions are summarized (Fig. 3). While it is not possible to analyze their data at the level undertaken for amphibians and reptiles, it seems clear that the pattern for angiosperm distribution is remarkably similar. In my opinion, a detailed analysis of generic distributions for the area would provide even stronger confirmation for my re-interpretation of their data as outlined below.

Raven and Axelrod (1974: 627–630) recognized several components in the Central American flora: 1) a group of 51 families of clear South American affinities, many of which were in North America by Eocene times, but others that were Isthmian Link dispersers; 2) a series of 9 southern families thought to have been present in North America by early Tertiary; 3) a group of 54 families of northern origin, about 40 of which range south, at least to Panama; 4) a group of 25–30 families of apparently northern affinities that dispersed across the Isthmian Link, southward in Pliocene to Recent times; and 5) a group of 11 families of

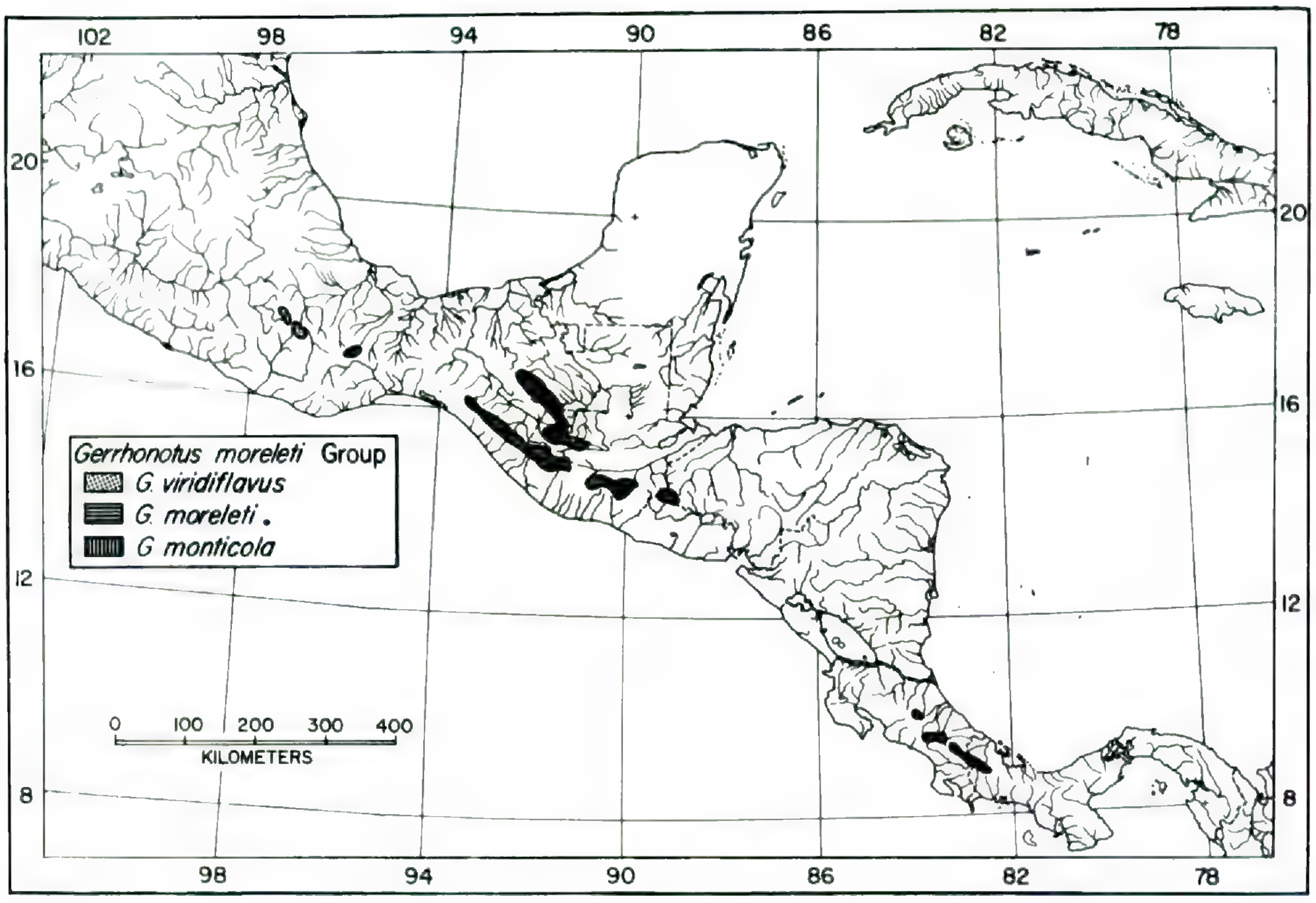


FIGURE 23. Distribution of the alligator lizards allied to *Gerrhonotus moreleti*, showing fragmentation of once continuous range by uplift of the Mesoamerican montane regions.

northern origin that seemed to have arrived in South America prior to the appearance of the Link. In addition, they list a group of 14 families endemic chiefly to semiarid to arid regions of North and Mesoamerica. The latter two components are uninformative to the problem at hand and will not be discussed further.

Although the various groupings proposed by Raven and Axelrod are ambiguous, they are informative. The data indicate, clearly, that Central America contains angiosperm stocks of both northern and southern affinities. A major cluster of southern families (many in group 1 and all in group 2) were in Central America by Oligocene, where they underwent differentiation in isolation from their sister groups in South America. The picture presented by Raven and Axelrod, for these groups, is obscured somewhat by their failure to sort out post-Miocene dispersers that reached Central America and South America across the Isthmian Link and those that had arrived earlier. Nevertheless, these families conform exactly in distribution to the South American-Caribbean track (for the sister taxa isolated in South America) and the Middle American-Caribbean track (for those isolated in America north of the Panamanian Portal during most of Tertiary); i.e. they correspond to the South American and Middle American herpetofaunal elements described above.

It will be no surprise to the reader that components 3 and 4 are interpreted as equivalent to the Old Northern Element of the herpetofauna, since they conform to the North American-Central American track (Fig. 12). In addition, Axelrod (1975) has conclusively demonstrated the reality of, and explained the his-

tory for, the floral equivalent of the Central American herpetofaunal component of this northern element, which includes such genera as *Acer, Carpinus, Carya, Cornus, Fagus, Ilex, Liquidambar, Myrica, Nyssa, Prunus,* and *Tilia.*

Bussing (1976) briefly reviewed the distribution and history of the freshwater fishes of Middle America, with major emphasis on the San Juan province (Fig. 4). He recognized two major distribution patterns for Central America: 1) Old Southern: a diverse series of genera most closely allied to South American sister groups, thought by Bussing to have been isolated in Central America from Eocene onward; and 2) Young Southern: recent trans-Isthmian dispersers from South America. In addition, he refers to a single Old Northern taxon, the gar, *Lepisosteus.*

It is apparent that the Old Southern Element of Bussing corresponds directly to the Middle American Element and track recognized for the herpetofauna (Fig. 14) and that the Young Southern Element represents the South American-Caribbean track (Fig. 13). Northern freshwater fishes are poorly represented in Central America, but *Lepisosteus* and several other genera conform to the North American-Central American track (Fig. 3).

An analysis of the data for the Mesoamerican region contained in Miller (1966), Martin (1972), Bussing (1976), and Rosen (1976) makes it possible to identify the component freshwater fish genera of each of the three Central American Elements (Table 6). Martin, Bussing, Rosen, and I agree that the somewhat artificial categorization of freshwater fish families into primary (not entering saltwater) and secondary (some members occasionally entering brackish or ocean waters) divisions is inappropriate primarily because some representatives of the former division are now known to have considerable salt tolerance. In addition, almost all species of the secondary division are restricted to freshwater and their patterns of distribution conform to those for primary division taxa. Obviously, marine fishes that frequently migrate or immigrate into freshwater (peripheral division) are not included in the analysis.

Bussing (1976) developed a strong argument for a late Cretaceous land connection between Central and South America that allowed freshwater fishes to invade the former from the south (dispersal). He effectively counters the argument that the ancestors of the Middle American Element could have arrived by swimming through an extensive saltwater barrier. The Middle and South American units were isolated, according to Bussing's concept, by a marine portal (vicariance), during most of Cenozoic, and have now only recently come back into contact along the Isthmian Link. Except for the usage of a different terminology for his historical source units, Bussing's model conforms exactly to that described above for the herpetofauna and suggested for flowering plants. The model includes a single major dispersal of southern taxa into Central America, followed by a major vicariance event to fragment Middle and South American components. Subsequently, northern stocks (in the case of fishes, very few) became associated with the Middle American unit. On the emergence of the Isthmian Link, South American taxa have invaded lower Central America to some degree and there has been a minor reciprocal dispersal of Middle American stocks southward.

TABLE 6. Component genera of principal historical units of the Central American freshwater fish fauna.

Old Northern (3)	Middle American (32)	South American (42)
Gar:	Characins:	Characins:
Lepisosteus	*Hyphessobrycon* (pt.)	*Apareiodon*
Catfishes:	Gymnotids:	*Astyanax*
Ictiobus	*Gymnotus* (pt.)	*Bramocharax*
Ictalurus	Catfishes:	*Brycon*
	Rhamdia (pt.)	*Bryconamericus*
	Killifish:	*Carlana*
	Cyprinodon	**Characidium*
	Floridichthys	**Compsura*
	Fundulus	**Creagrutus*
	Garmanella	**Ctenolucius*
	Oxyzygonectes	**Curimata*
	Profundulus	**Gasteropelecus*
	Rivulus (pt.)	**Gephyrocharax*
	Four-eyed Fishes:	**Hemibrycon*
	Anableps	**Hoplias*
	Viviparous Tooth-Carps:	**Phenagoniates*
	Alfaro	**Piabucina*
	Belonesox	**Pseudocheirodon*
	Brachyrhaphis	**Rhoadsia*
	Carlhubbsia	**Roeboides*
	Gambusia	Gymnotids:
	Heterandria	**Sternopygus*
	Heterophallus	**Hypopomus*
	Neoheterandria	**Eigenmannia*
	Phallichthys	**Apteronotus*
	Poecilia	Catfishes:
	Poeciliopsis	**Trachycorystes*
	Priapella	**Ageneiosus*
	Priapichthys	***Imparales*
	Scolichthys	**Pimelodus*
	Xenodexia	**Pimelodella*
	Xiphophorus	**Pygidium*
	Cichlids:	**Hoplosternum*
	Cichlasoma (pt.):	**Astroblepus*
	Amphilophus	**Hypostomus*
	Archocentrus	**Chaetostoma*
	Herichthys	**Ancistrus*
	Paraneetroplus	**Lasiancistrus*
	Parapetenia	**Leptoancistrus*
	Theraps	**Loricaria*
	Thorichthys	**Sturisoma*
	Petenia	Cichlids:
	Neetroplus	**Aequidens*
	Herotilapia	**Geophagus*
	Synbranchids:	Synbranchids:
	***Ophisternon*	*Synbranchus*

(pt.) = different species group in South America.
* Restricted to lower Central America.
** Same species disjunct in South America.

The distributions of recent and fossil mammals for the region have been extensively reviewed by several workers, most recently by Savage (1974), Ferrusquia-Villafranca (1978), and Marshall et al. (1979). These studies all confirm that the South American mammal fauna was isolated from that of Central America until Pliocene; that no distinctive Middle American mammal fauna can be recognized; that no cluster of taxa of southern relationships, equivalent to the Middle American unit seen in the freshwater fishes and herpetofauna, can be distinguished; and that the region was dominated by groups of northern affinity until the interchange with South America from Miocene onward (Fig. 4).

On the other hand, a cluster of distinctly tropical groups with northern affinities seems to have been established in Central America by the end of Eocene. Some of these represent endemic genera, others were among the first northern invaders across the Isthmian Link when it became emergent. Still others of more temperate affinities remained in Central America or dispersed across the Link to South America (Table 7). The first two groups and possibly the third are equivalent to the Central American Component of the herpetofauna. All four groups lie on the North American-Central American track (Fig. 12).

In addition to his consideration of amphibians, reptiles, and freshwater fishes, Rosen (1976) utilized the distributions of other organisms in the development of his vicariance model of Caribbean biogeography (Figs. 5, 24). As pointed out above, Rosen's South American-Caribbean track is a composite of the isolated fragments (in Middle and South America) of an ancient vicariance event with an overlay of trans-Isthmian dispersal. For example, the distribution of the frog genus *Leptodactylus* (Rosen's fig. 2c) and the fish genus *Synbranchus* (fig. 2f) appear to lie on the same track as the onychophoran genus *Peripatus* (fig. 2b). The former are recent dispersers across the Isthmus; the latter represents an ancient track with endemic Middle and South American components. An additional difficulty with Rosen's data is his confusion of several clearly Middle American stocks (i.e. ones derived from southern sources and affected by the major ancient vicariance event that separated the Americas) with his North American-Caribbean track. He points out the composite nature of this track by referring to an older Laurasian component and a younger Gondwanian one. Review of his examples indicates that the so-called Gondwanian component is comprised of taxa with closest affinities to South American stocks, i.e. they correspond to the Middle American-Caribbean track (Fig. 14) and are equivalent to the Middle American Element described above for freshwater fishes, amphibians, and reptiles. The most important examples of this pattern mentioned by Rosen are cyprinodontid and poeciliid fishes (his specialties). A reordering of Rosen's data, with these points in mind, produces a pattern conforming exactly to that described above for herpetofaunal and freshwater ichthyofaunal development. Rosen's ideas of an ancient major dispersal event from South to Central America, followed by a major vicariance event (the development of the Panamanian Portal) are in complete agreement with herpetofaunal data. In addition, Rosen (1978) further confirms and supports the concept of the incorporation of a distinct Old Northern component into the Mesoamerican biota in Eocene as proposed by Axelrod (1975) and Savage (1966). He agrees that this component became isolated by a disjunc-

TABLE 7. Central American terrestrial mammalian faunal components (bats excluded).

South American	North Tropical	North American
Marsupials: Didelphidae Primates: Callithricidae (marmosets) Cebidae (monkeys) Xenarthran edentates: Dasypodidae (armadillos) **Glyptodontidae (glyptodonts) **Megalonychidae (ground sloths) **Megatheriidae (ground sloths) Bradypodidae (tree sloths) **Mylodontidae (mylodonts) Myrmecophagidae (ant-eaters) Caviomorph rodents: Echimyidae (spiny-rats) Dasyproctidae (aguti) Cuniculidae (paca) Hydrochoeridae (capybara) Erethizontidae (porcupines) Sigmodontine mice (*Nyctomys*, *Otonyctomys*, *Oryzomys*, *Sigmodon*)	1. Into South America a squirrel (*Sciurillus*) tropical dogs (*Dusicyon*, *Chrysocyon*, *Atelocynus*, *Speothos*, *Lycalopex*) spectacled bear (*Tremarctos*) Procyonids (**Cyonasua*, *Nasua*, *Potos*, *Bassaricyon*) Mustelids (*Lyncodon*, *Galictis*, *Eira*, *Pteronura*) cats (***Smilodon*, some *Felis*) **mastodons (Gomphotheriidae) **horses (Equidae) tapirs (Tapiridae) deer (*Mazama*, *Pudu*, *Hippocamelus*, *Blastocerus*, *Blastoceros*) *camels (*Lama*, *Vicugna*) 2. Endemic to Central America a squirrel (*Syntheosciurus*) gophers (*Orthogeomys*, *Heterogeomys*, *Macrogeomys*) a heteromyid (*Liomys*) a peromyscine mouse (*Scotinomys*) a neotomine mouse (*Otoylomys*)	1. Into South America a shrew (*Cryptotis*) rabbits squirrels heteromyids (*Heteromys*) peromyscine mice (*Aporodon*) a neotomine mouse (*Tylomys*) gray fox (*Urocyon*) raccoons (*Procyon*) weasels (*Mustela*) otter (*Lutra*) skunk (*Conepatus*) cats (several *Felis*) 2. In Central America flying squirrel (*Glaucomys*) peromyscine mice (*Baiomys*, *Reithrodontomys*, *Peromyscus*) neotomine mice (*Neotoma*) voles (*Microtus*) coyote (*Canis*) cacomistle (*Bassariscus*) skunks (*Mephitis*, *Spilogale*) **mastodon (Mammutidae) **mammoth (Elephantidae) **rhinoceros (Rhinocerotidae) **Protoceratidae **oreodonts (Merycoidodontidae) *bison (Bovidae)

* Extinct in area.
** Extinct in New World.

tion, across the south-central region of what is now the United States, from its congeners in eastern North America and evolved in coexistence with the Middle American Element. Recent dispersals across the Isthmian Link are responsible in Rosen's theory for sympatry among related taxa in lower Central America and northwestern South America.

To summarize: a reanalysis of data for angiosperms and vertebrates indicates that the major distributional pattern outlined for herpetofaunal development forms a repetitive general pattern for all groups except mammals. That angiosperms, freshwater fishes, amphibians and reptiles are congruent in generalized tracks that seem to have originated through the same series of dispersal and vicariance events is remarkable. That the mammal pattern is different is interesting and suggests strongly that mammals of modern type, except for marsupials, were not present in the Americas at the time when the major vicariance event, isolating Middle from South America, took place.

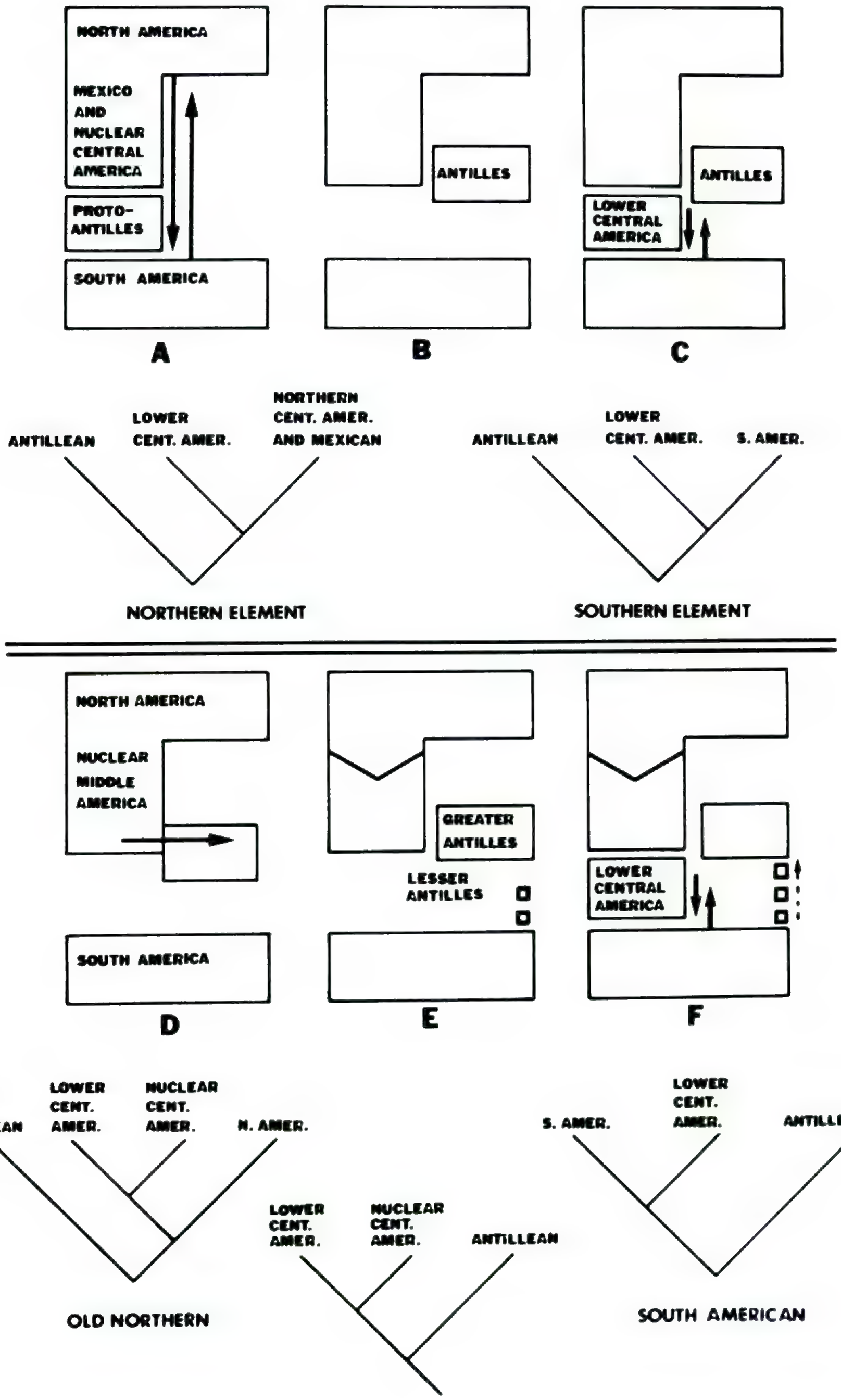


FIGURE 24. Simplified models of Middle American biogeography. Upper, a vicariance model of Caribbean biogeography, after Rosen (1976); lower, revised model proposed here and described in text. Predicted phylograms for taxa occurring in the indicated areas are indicated below models. Arrows indicate dispersal events.

SPACE, DISPERSAL, VICARIANCE, AND TIME

The first concern of historical biogeography is the search for patterns of phylogenetic relationship that establish connections between biotas in time and space. For the devoted reader who has followed the arguments presented in the preceding sections, it will be a relief and a bemusement to realize that it has taken to this point in the paper to establish the patterns. We may now return to the second concern of biogeography: by what processes were the pattern developed? I wish to state at the outset that I do not believe that it is possible to produce an analysis of process that will explain the distribution of every taxon, nor do I believe that a common distribution pattern is always the product of a single causal event. Neither do I accept *a priori* that the dogma of vicariance or the tenets of revised dispersal theory offer a totally satisfactory means for explaining patterns. Nevertheless, it seems clear that cladistic analysis of relationships for organisms having common distribution patterns can discern repetitive general relationships among areas that will point to common causal events. In general, I expect about 80% of the taxa in a biota to conform to one or the other of several congruent general patterns of phylogenetic-area relationships. These patterns are the ones with common causes that may then be sought in earth and climatic history.

I believe that the account, to this point, has conclusively demonstrated three general patterns of distributional history in Central America. These general patterns require an ancient concordant dispersal event of southern groups into Central America, followed by a major vicariance event that fragmented the original stocks into Middle American and South American units. A second concordant dispersal established northern groups in the region and these groups (and their Middle American associates) were isolated by a second vicariance event from northern congeners. Finally, a late Tertiary reconnection between Central and South America is required to allow for a major dispersal (interchange) of formerly isolated and endemic taxa between the two regions (Figs. 12–15).

These events may be arranged in a chronological order as follows:

Dispersal I—from south
Vicariance I—between Central and South America
Dispersal II—from north
Vicariance II—between tropical Mesoamerica and North America
Dispersal III—from south

In search for historical processes, the events may be considered in reverse chronological order, since the more recent ones may be less concealed by the modification and distortions produced by time. It is also important to remember that the events cover a range of time, going back to the Cretaceous, when the earliest fossils of almost all the main lineages of amphibians and reptiles in the region make their appearance in the fossil record of North or South America (Table 3). Most of the broad features of Cretaceous to Pliocene historical geology and climate for Middle America have been discussed previously or earlier in the present paper (Savage, 1966; Axelrod, 1975; Bussing, 1976; Rosen, 1978, fig. 15) and the reader is referred to them for background. It is from among these features that the progenetic causes of current patterns will be sought.

Dispersal III is so clearly and unquestionably associated with the emergence of the Isthmian Link in Pliocene that it hardly needs comment. The only question at issue remains the time of the actual final closure of the Bolivar Trough, the most southern and last marine barrier to be uplifted and to complete the land connection. In essence, the Link developed from north to south, beginning in Oligocene, when a series of volcanic islands formed in the Portal Zone. A long narrow peninsula extended continuously from Nuclear Central America to the eastern Panamanian area by late Miocene (Malfait & Dinkelman, 1972). Marshall et al. (1979) claimed that closure was not completed until late Pliocene, about 3 m.y. B.P., on the basis of mammalian fossil correlations. Others (Raven & Axelrod, 1974; Savage, 1974) placed the closure in earliest Miocene, now dated as about 5.7 m.y. B.P.

While the differences in date of closure may be of relatively little importance in the present context, it is significant in any discussion of South American biogeography. The mammal argument is based upon the first appearance of North American groups in temperate zone Argentina, about 3 m.y. B.P. South American groups first appear in the southern United States about 2.5 m.y. B.P. Both United States and Argentine localities are several thousand kilometers from the Isthmian Link. I continue to argue that it would take considerable time for dispersal across the vast intervening areas of tropical America and the diverse ecological settings between the Isthmus and Argentina, Arizona, Texas, or Florida, in order to make possible an occurrence in the fossil record of these places about 3 m.y. B.P. Finally, the records of North American mammal groups, in the late Miocene of Central Panama (Whitmore & Stewart, 1965), further support the idea of closure of the portal at that time to allow 5.7 million years for dispersals across the Isthmus in both directions.

The events of Dispersal II and Vicariance II, which involved dispersal of northern stocks into Middle America and their subsequent disjunction from allied groups in eastern North America and differentiation in isolation, have been reviewed above in several contexts. All evidence (Savage, 1966; Axelrod, 1976; Rosen, 1978) places the dispersal event as prior to Eocene and the vicariance event as associated with mountain building and cooling and drying trends that were instituted in Oligocene. The trends produced a strong climatic barrier of temperate semiarid to arid situations between Middle America and the fragmented northern temperate forest regions by mid-Oligocene (Fig. 2).

Vicariance I seems to be based upon the long isolation of Central and South America prior to the formation of the present Panamanian Isthmus. Evidence from all studied groups, except for placental mammals, strongly supports a relationship between many Middle American stocks and South American taxa, that is prior to and not the result of the most recent dispersal event (III). Dispersal I must have occurred from south to north prior to the differentiation of Middle and South American congeners showing this pattern. The question remains, how did the initial dispersal occur and what event or events led to the fragmentation of Vicariance II?

In 1966, based upon the herpetofaunal evidence and then current ideas on the geology of Central America, I proposed that a Paleocene intercontinental connection existed with South America (Fig. 2). This land connection provided the

route for southern groups to enter Central America (Dispersal I) and its subsidence initiated differentiation (Vicariance I). Most recent geologic studies (Holden & Dietz, 1979; Malfait & Dinkelman, 1972; Ladd, 1976) concur in rejecting any notion of such a connection from early Cretaceous to Pliocene, a time span of over 100,000 m.y.

Rosen (1976) and Duellman (1979) have used the concept of a late Cretaceous-Paleocene series of islands (the proto-Antilles), lying in the region between Nuclear Central America and South America, to explain the distributional phenomena described in this report. Rosen argued for a single concordant dispersal (I) of many southern groups across these islands, which subsequently move eastward with the Caribbean plate to isolate Central and South America (Vicariance I); see Fig. 5. Duellman, on the other hand, advocates numerous dispersals across the proto-Antilles and the later emergent Middle American archipelago, which ultimately became the Isthmian Link. I have dealt, in some detail, with this idea and its rejection in an early section, and so will not repeat it here. Essentially, Rosen's explanation is by vicariance, Duellman's by long-distance dispersal by individual taxa. What concerns us here is not these points, but the reality of the proto-Antilles and their possible role in Dispersal I and Vicariance I.

Pregill (1981), utilizing the data and interpretations of Perfit and Heezen (1978) and a re-reading of Malfait and Dinkelman (1972), concluded that no evidence exists for the presence of any precursors of the Antilles in the Panamanian Portal region at any time. According to this explanation, both Greater and Lesser Antilles are oceanic islands of separate origins and history and cannot be origins significant to the biotic interchanges affecting Middle America. In Pregill's view, as predicted by Patterson (1981) earlier, Rosen's model of vicariance biogeography for the Caribbean, and especially the Antilles, does not stand up to scrutiny in the light of new tectonic and geologic evidence as cited by them and in the earlier section on the nature of this problem in this paper. The result leads to the conclusion that the Panamanian Portal was an open seaway during Paleogene times and only later was a potential dispersal route for island-hopping individual taxa across the Middle American archipelago.

Nevertheless, the evidence of biogeography is incontrovertible in indicating a former ancient continuity between Central and South America, the concordant dispersal (I) of southern groups northward into Central America during this continuity, and the subsequent fragmentation of continuity by a major vicariance event (I). Both dispersal and vicariance obviously occurred prior to Eocene times.

Several groups of earth scientists have proposed alternate configurations of Caribbean geological history that may contribute to resolving this problem. These include traditional (plate-tectonic influenced) workers (Lillegraven et al., 1979; Melville, 1981) and advocates of the expanding earth hypothesis (Owen, 1976; Carey, 1976; Shields, 1979). The first proposed that an archipelago existed from Cretaceous to Eocene that extended from northern Venezuela across the Caribbean Sea to the Nicaraguan Plateau (now submerged) and included the Aves Arc Islands (now submerged) and volcanic islands that were probably the predecessors of the Greater Antilles.

Melville (1981), using the paleomagnetic data from Steinhauser et al. (1972) and Gose and Swartz (1972) rotated the Greater Antilles by about 45° to bring

Cuba and Yucatan into contact and established a continuous connection between Colombia and Central America for Paleocene.

Shields (1979) regarded the Greater Antilles as continental fragments that were originally connected to Nuclear Central American blocks, the Lesser Antilles, and northern South America. In his view, as the Caribbean Sea was formed, beginning in Late Cretaceous (65–75 m.y. B.P.), these several blocks became fractured with the Nicaraguan block and Rise, separating from Venezuela at this time. Separation of the Greater Antilles and Nicaraguan Plateau from one another was probably in Paleocene or even as late as Eocene. Thus, there was a continuous land connection well to the east of the present day Isthmus in late Mesozoic to Paleocene times, which included the Greater Antilles and, possibly, the Lesser Antilles as well. Subsequently, Tertiary events destroyed the connection and further distorted the geographic relations of the insular components into their present configurations.

Coney (1983) in the present symposium argues convincingly for the presence of a proto-Greater Antilles-Aves Arc Island chain lying between Nuclear Central and South America in late Mesozoic-Paleocene time. Subsequently, according to this interpretation, the system moved northeastward, apparently in close proximity to the Guatemala-Yucatan component of Nuclear Central America. The southwestern extension of this system was probably the Aves ridge islands and Cordillera Costeña of northern Venezuela. By Eocene the proto-Greater Antilles had stabilized near their present geographic position with the Lesser Antilles appearing in association with an east-facing subduction zone (Puerto Rican Trench) that began to consume Atlantic Ocean floor. The movement of North and South American plates westward past a nearly stationary Caribbean plate fragmented the Greater Antilles into their present pattern. While this interpretation was not available to me prior to writing the following sections of the present paper, note how well Coney's ideas on Greater Antillean history correspond to the model developed from plant and animal distributions below (Fig. 24).

These references confirm the conflicting ideas concerning the geologic history of the region, but suggest that emerging lines of evidence raise the possibility of a Late Cretaceous-Paleocene land connection between Nuclear Central and South America, lying to the eastward of the present Isthmus. While the evidence for any particular model of the origin and history of such a connection does not seem overwhelming, and since I am unable to evaluate the several conflicting geological interpretations, I will not choose among them. Any of them, however, provides a geographic basis for Dispersal I and Vicariance I.

After reaching this point in the discussion of Central American biogeography, I once again re-evaluated the distributional data to confirm the reality of the patterns and the necessity for a pre-Eocene Dispersal I and Vicariance II to explain them. I was somewhat encouraged by the comments of Melville (1981) that paleontology and plant distributions supported the idea of a Paleocene connection between Central and South America. I was further encouraged by the discovery that Howard's (1973) review of Caribbean plant distributions, which I had overlooked previously, showed patterns similar to those described above for other organisms when generic ranges were studied. He recognized two primary mainland units, a western and a southern continental, that conform closely to the

Middle and South American units, recognized throughout this paper, respectively. After all this, I cannot but conclude that the concordant patterns are generalities requiring explanation and that the explanation requires a pre-Eocene Dispersal I and Vicariance II.

Biogeography, if it is a science, must be able to predict pattern from pattern and estimate process from pattern. In the present case, there remains no recourse but to predict that: there was *a continuous land connection or series of proximate islands extending from northern South America to the area of Nicaragua in late Mesozoic and/or early Tertiary*.

This land connection or island archipelago seems to have included the future Greater Antilles that were closely associated with the Nicaraguan region. Subsidence and reorientation of the components of this connection in late Paleocene were responsible for Vicariance I. Dispersal I occurred across this connection prior to that time. It will be noted that subsidence and distortion of the proposed connection probably occurred from south to north and the final fragmentation involved separation of the Greater Antilles from one another and the other blocks, in early Tertiary.

THE ANTILLES REVISITED, BRIEFLY

When I first began this review of Central American biogeography, it was without any intention of treating the Greater and Lesser Antilles and their relationship to the mainland. My original intention has not been fulfilled for an understanding of the history of the herpetofauna of Central America leads, naturally, to a consideration of Antillean patterns. This is especially so because of Pregill's (1981) critique of Rosen's vicariance model, which attempts to deny the empirical reality of the biotic patterns established above and to invoke a special dispersal theory for the Antilles. Pregill correctly pointed out that some geologic evidence does not support the notion of a proto-Antilles that lay between Nuclear Central America and South America in late Mesozoic-Paleocene times. The presence of these islands and their subsequent movement north and eastward were the cornerstone of Rosen's vicariance model. It was across these stepping-stones that he thought southern taxa had invaded Central America. In addition, because of their relationships to that region and South America, Rosen believed that the northern and southern faunal elements, now found in the Antilles, rode the drifting proto-Antilles as the Caribbean plate moved eastward (Fig. 5 summarizes this model).

Coney (1983) in the present symposium, has effectively countered Pregill's argument and shown that a proto-Greater Antilles-Aves Ridge-northern Venezuela chain of islands doubtless existed in late Mesozoic-Paleocene times. He further demonstrated that this chain lay between the Guatemala-Yucatan portion of Nuclear Central America and northern South America and that the proto-Greater Antilles had a close association with the latter block until middle or late Eocene. He further confirms that the Lesser Antilles are a more recent development of volcanic origin associated with the east-facing subduction zone where Atlantic oceanic crust is consumed along the margin of the Caribbean plate. This interpretation differs from Rosen's (1976) model principally in regarding the Greater

and Lesser Antilles as independent of one another, relating the island chain of Cretaceous-Paleocene times with the Guatemala-Yucatan portion of Central America and having the southern terminus of the arc in what is now Venezuela.

Pregill's other main points against Rosen's proposals are more arguable: 1) that the present fauna of the islands arrived by overwater dispersal from Oligocene onward because many of the Antillean groups are not known prior to that time as fossils in North or South America; 2) that certain major groups, especially of marsupials, carnivores, and ungulate mammals are absent from the islands and unknown as fossils there; a situation that is unlikely, if a land connection or proximate series of islands connected the Antilles to other major land masses; and 3) the current fauna contains remarkably few major (orders, families, and genera) groups and those groups that are present have uneven distributions among islands; again, suggesting overwater dispersal to oceanic islands.

The arguments are all specious. It is clear from accumulating evidence, as emphasized by Rosen (1978), that almost all extant major groups of freshwater fishes, amphibians, and reptiles were present in the Americas by Eocene and that most families go back to Cretaceous. The incomplete fossil record on both the mainland and in the Antilles can only provide us with minimum ages for the presence of groups in these areas and some record of extinctions (Patterson, 1981). It cannot provide direct evidence of mode or time of dispersal, although it may aid in choosing among geological events of different ages that allowed concordant dispersal and created vicariance events. In this regard, I have accepted the view of vicariists that paleogeography and paleoclimatology, not fossils, are arbiters of biogeographic history.

Pregill's second point is also untenable. The absence of groups from the fossil record of an area, especially a lowland tropical one, tells us very little about the history of its biota. There are no fossil records in Central America of marsupials, bats, primates, non-caviomorph rodents, most families of carnivores and ungulates, and almost all families of amphibians and reptiles that occur there today. Does this mean that none of these groups occurred there until very recently? Or tell us at what time they appeared in the region? There are hardly any records of fossil vertebrates from tropical South America, including most families present there today. Does this mean that the missing groups were absent from the region?

In regard to Pregill's final point, it is obvious that the present fauna of the Antilles is not a full-fledged continental one and that some groups may have arrived relatively recently by overwater dispersal. It must also be noted that there is a record of extensive late Pleistocene to Holocene extinctions for the Antilles in which primates and edentates died out along with many other forms (Simpson, 1956; Pregill, 1981). Earlier extinctions cannot, of course, be ruled out as a factor in contributing to the unbalanced nature of the biota, and I must conclude that neither the current decimated fauna nor the fossil record conclusively require a special dispersal theory as proposed by Pregill. He follows the time-honored procedures of conventional biogeography: 1) recognize an individual pattern, 2) elaborate a process (in this case, special dispersal), 3) use the process to explain the pattern, and 4) extend the process to explain other similar patterns (each dispersal by individual taxa).

The vicariance approach, on the other hand, 1) recognizes an individual pat-

tern of phylogenetic-area relationships (Fig. 7), 2) hypothesizes a process, 3) tests the hypothesis with more analyses of phylogenetic-area relationships, 4) accepts or revises the hypothesis, and 5) tests it again with additional phylogenetic-area relationships. This approach is the one advocated by Rosen (1976) and used to test his vicariance model for the Caribbean (Fig. 24). Since the lynchpin of that theory was the proto-Antilles hypothesis and that hypothesis has proven unsound, a brief review of an alternate explanation seems in order.

As discussed in a previous section, Rosen's grouping of the Middle American and South American units of this report on a single track (the South American-Caribbean) and his failure to place the so-called Gondwanian component of his northern track as separate from the Laurasian component obscured the discreteness of the three principal units recognized for Central America, in the present account. Once these units (tracks) have been clearly defined (Figs. 12–14), a coherent explanation of Antillean biogeography emerges (Fig. 24).

Whether or not the Greater Antilles were involved in a land connection between Central and South America, in Cretaceous or Paleocene, it is clear from the geologic evidence cited above that they or their precursors were closely proximate to the Nicaraguan region in early Tertiary, if not physically continuous with it. Volcanic activity, initiated in Cretaceous, was extensive across the region and partially distorts any interpretation of succeeding events. This proximity would allow for the dispersal of Middle American Element taxa onto the peripheral continental fragments that became the Greater Antilles. A few North American Element taxa also reached the Greater Antilles at about the same time, possibly in the Eocene (Shields, 1979), when the Central American component became associated with Middle American taxa on the mainland. These events would explain the closer biotic relationship between the western Greater Antilles, particularly Cuba, and North and Middle America, commented on by Rosen (1976). Subsequently, the several Greater Antillean blocks, including the Nicaragua Rise and Cayman Ridge, were separated or further removed (about 200 km eastward) from proximity to the Nuclear Central American region and affected by the events described by Pregill (1981), as interpreted from Perfit and Heezen (1978), for the post-Oligocene time-frame.

Whatever their possible role in any postulated late Mesozoic-early Tertiary land bridge or archipelago in the region between Central and South America, the Lesser Antilles seem to have had a separate history from the Greater Antilles for most of Tertiary (Malfait & Dinkelman, 1972). The islands are a mostly volcanic arc associated with the zone where Atlantic oceanic crust subducts under the Caribbean plate. As such, they were preceded by the late Cretaceous-Paleogene Aves Arc Islands that originally lay 200 km westward, and that marked an earlier boundary position of the eastward moving Caribbean plate. Dispersal from South America onto the Aves Arc, and then across subsiding stepping stones onto the present Lesser Antilles, as proposed by Rosen and supported by Pregill's discussion, explains the presence of predominately southern groups in these islands.

This model also explains why no northern stocks reached South America in early Tertiary. They simply were not yet in Nuclear Central America. Thus, it avoids the problem of one-way dispersal from south to north required by Rosen's confusion of Middle American and Old Northern Elements on his North Amer-

ican-Caribbean track and his failure to separate Middle American and South American Element tracks from one another. It in no way affects the following conclusions: 1) the Lesser Antilles have been populated by overwater dispersal from the south; 2) the Greater Antilles received the nucleus of their herpetofauna by a single concordant dispersal event from Central America by both Old Northern and Middle American taxa; and 3) other groups of organisms show a similar set of general patterns.

The model described above (Fig. 24) forms my hypothesis of the process responsible for the history of the Caribbean biota. It explains the failure of Old Northern taxa to reach South America early in Tertiary, the presence of Old Northern taxa in the Greater Antilles, the differences between the biotas of the Greater and Lesser Antilles, and the great similarity of the Cuban biota to that of Nuclear Central America. Further, it predicts that 1) the Greater Antillean biota, especially that of Cuba, is older than the lower Central American biota; 2) the Lesser Antilles biota is mostly derived from South American groups and is relatively older than South American representatives in the lower Central American biota; 3) some components of the Greater Antillean biota (Middle American unit) are equal in age to that of Nuclear Central American sister taxa, but younger than their sister groups in South America; and 4) some components of the Greater Antillean biota (Old Northern unit) are older than Nuclear Central American sister taxa, but are equal in age to their sister groups in North America. In other words, if a monophyletic group shows a vicariance pattern in the region, lower Central American taxa will show greater affinity to mainland taxa to the north or south than to Antillean taxa. Greater Antillean taxa will be found to be most closely related to Nuclear Central American taxa or these taxa plus their lower Central American sister groups (Middle American unit) or to North American taxa (Old Northern unit) and their Middle American sister groups. Lesser Antillean taxa will be found to be most closely related to South American taxa or these taxa and their lower Central American sister groups. Comparison of these sets of predicted relationships with Rosen's model summarizes the different concepts (Fig. 24). Predicted cladograms of phylogenetic relationships are included as well.

A review of the cladograms presented by Rosen (1976; fig. 21) is included for comparison with the revised model (Fig. 25). Additional data that aid in evaluating the figures include: A, the closest ally of *Lepisosteus tristoechus* is *L. spatula* of the southeastern United States, but recently discovered to have a disjunct population in lower Central America as well (Wiley, 1976), which, if added to the cladogram, conforms to the proposed model for Old Northern forms. D and E involve cases with an eastern North American form of Central American and/or Antillean affinities, so that the cladograms alone will not resolve their geographic relationships from those of the Old Northerners; since we now know that these groups are anciently related to southern stocks and are part of the Middle American unit, they should fit the Middle American cladogram; D may, E does not, suggesting a possible dispersal event. F appears to conform to a cladogram indicating the ancient interrelationship of a Mesozoic-Paleocene neotropical fauna (Fig. 18) and is compatible with the cladogram for Middle American Element groups (these, too, would ultimately have a South American sister group). The other cladograms (B, C, G) agree with the one for the Middle American unit.

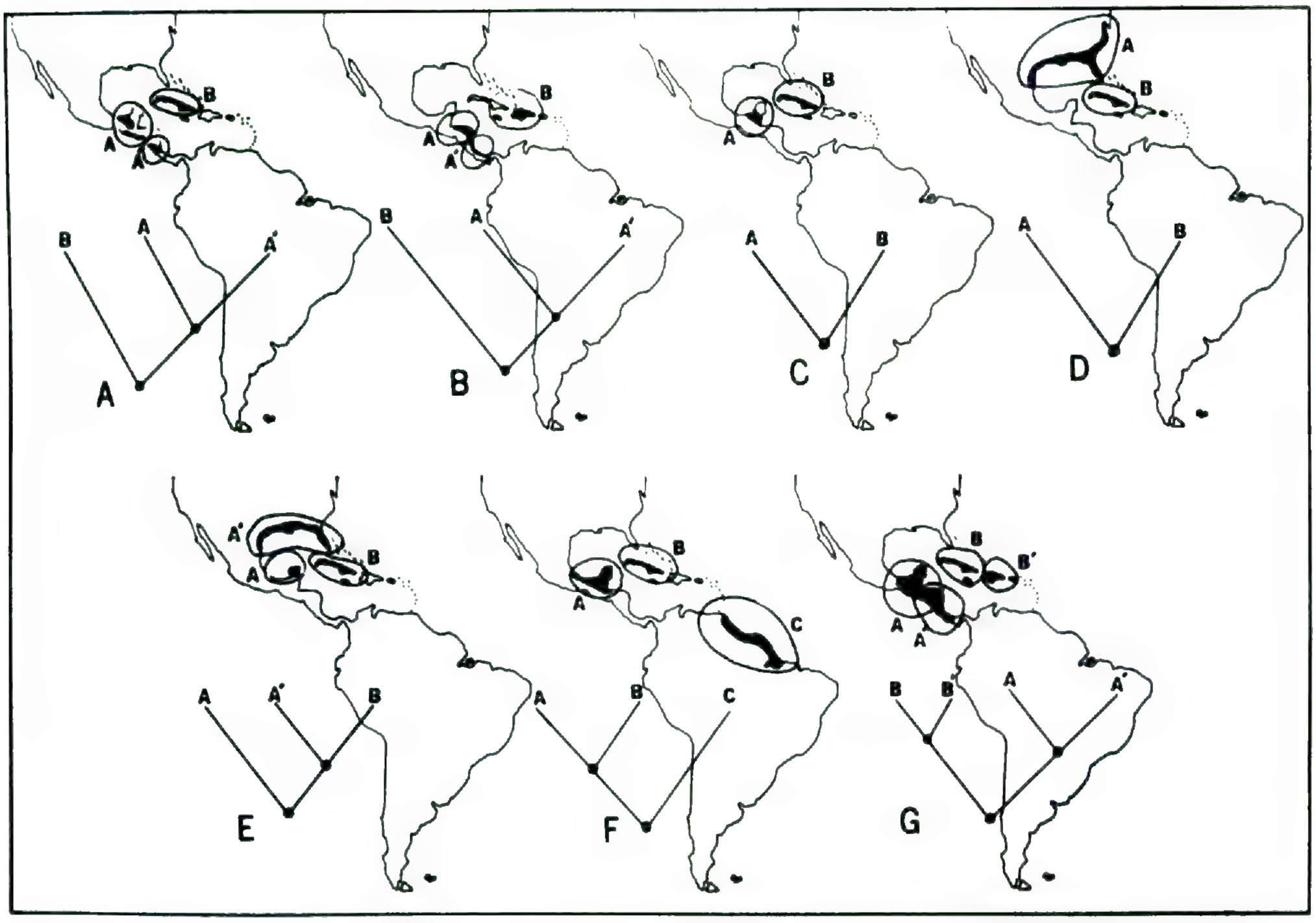


FIGURE 25. Phylograms of taxa used by Rosen (1976) in support of his vicariance model. A, garfishes, genus *Lepisosteus*; B, viviparous tooth-carps, *Gambusia nicaraguensis* group; C, viviparous tooth-carps, tribe Girardini; D, killifishes, genera *Lucania* and *Cubanichthys*; E, killifishes, genus *Fundulus*; F, the synbranchid eel, *Ophisternon*; G, cichlid fishes, genus *Cichlasoma* (*Parapetenia*). See text for revised interpretation of phylograms in relation to biogeography model in Fig. 24 (lower).

It appears from these examples that the model (Fig. 24) has considerable predictive value, explains the patterns and cladograms established by Rosen (1976), and avoids the necessity for positing a pan-Antillean archipelago in the history of the Greater Antilles. It, moreover, predicts that the nucleus of the Greater Antillean biota was present in those areas at least by late Eocene and probably sooner and confirms Rosen's (1978) insight that the observed biological patterns for the region have developed over a great time span, involving geologic events of at least the last 80 million years. Additional testing of the model requires cladistic analysis of the phylogenies of other taxa, especially those with relatives in all five areas, North America, Nuclear Central America, the Greater Antilles, South America, and the Lesser Antilles.

DISPERSALS, VICARIANCE, AND TIME

From the previous review of biogeographic pattern and the paragraphs above, it must now be clear that concordant dispersal and vicariance are two facets of the same process. It is not possible to have one without the other. For example, when the Panamanian Portal was removed as a barrier to terrestrial dispersal and became a land bridge between the Americas, the emergent Isthmian Link became, in turn, a barrier, vicariating the formerly continuous Caribbean-Eastern Pacific

biota. Dispersal to produce a generalized marine biota preceded the vicariant event. Vicariance in Middle and South America preceded the dispersal events that have taken place across the Isthmian Link to produce the great American interchange. The recognition of this point makes much of the argument between dispersal and vicariance biogeography moot.

If we may, then, rephrase the statements of biogeographic principle contrasted earlier (pp. 489–493), it may be possible to provide a basis for a biogeography that combines the best attributes of both approaches.

1–2. Concordant dispersal of many groups at about the same time is followed by vicariance to produce patterns.

3. Generalized source areas = centers of origin (i.e. Gondwanian, South American, Laurasian) may be estimated from track directionality.

4. Directionality of major dispersals may be estimated from generalized tracks, phylogenetic relationships, and paleogeologic and paleoclimatic relations.

5–6. Fossils provide evidence of extinctions, give minimum ages of occupation of areas, and permit a choice among geologic or climatic events of different ages as possible causes of biotic interrelationships.

7. Discovery of new fossils contributes data for testing biogeographic theory by adding new taxa for phylogenetic area analyses.

8. Relative age of groups (times of origin) important in explanation; fossils and their cladistic analysis contribute to estimating age.

9. Ecologic valence and associations relatively insignificant because they are epigenetic and correlate with present ecological and physiographic features (i.e. they are recent epigenetic modifiers of pattern); phylogenetic interrelationships and their relations to geography (past and present) crucial.

10. Concordant dispersal establishes basic pattern, then vicariance fragments continuity and allows differentiation of components of the pattern; random, long-distance, or multiple dispersals by individual taxa produce no repetitive patterns that can be tested.

11. Generally, allopatry indicates vicariance, and sympatry suggests vicariance followed by dispersal; parapatry and some sympatry suggests differentiation *in situ* by genetic means not associated with geographic or climatic barriers; at the time scale of most historical biogeographic studies, the latter events are unimportant.

12. The primary interest in historical biogeography is with progenetic processes.

13. Geologic evidence speaks for itself; continental drift must account for substantial and profound aspects of present patterns.

14. Both concordant dispersal and vicariance involved in patterns and process; plate movements and other geologic and climatic events that create and/or remove barriers contribute to pattern.

15. Individual taxa may show different patterns because of age; i.e. mammal and bird patterns not affected by the initial break-up of Pangaea while fishes, amphibians, and reptiles were.

16. Major patterns represent ancient disjunctions, other patterns represent more recent events; most major groups studied in terrestrial biogeography were present in Mesozoic or early Tertiary and progenetic events producing patterns occurred long before Quaternary.

17. Components (nodes) within tracks reflect the number of vicariance events usually produced by one concordant dispersal event.

18. Hypothesis tested by adding additional tracks, but only in a correlative way.

19. Lack of conformity with a well-documented generalized track suggests: a) the individual track belongs to another generalized track; b) it represents an independent dispersal; c) it is based upon a non-monophyletic group.

20. Hypotheses compared to earth's history to confirm correlations with opportunity for concordant dispersals and geologic and climatic vicariance events.

21. Predicts geologic and/or climatic history.

22. Predicts patterns for unstudied groups of approximately same geologic age; components of older groups may have patterns similar to those found in younger groups.

23. No prior judgement of former history of dispersals or geologic age of distributional events; these are discovered in a cladistic analysis.

24. A preferred method of analysis involves construction of cladograms of area interrelationships from cladograms of phylogenetic relationships (Fig. 7); a hypothesis of process is then constructed from paleogeologic and/or paleoclimatic evidence to conform with the area cladogram; the hypothesis is then tested (Fig. 24) by comparison of the phylogenetic relations for additional groups (Rosen, 1978; Platnick & Nelson, 1978; Morse & White, 1979; Patterson, 1981).

25. These approaches do not, by themselves, distinguish between concordant dispersal and vicariance, since they are so intimately interrelated, it does, however, provide a clear testable hypothesis of area interrelations, which usually will separate long-distance dispersal by individual taxa out from major pattern; knowledge of paleogeology and paleoclimatology may then aid in choosing among alternative dispersal and vicariance sequences and events.

In summary (Fig. 26), biogeographic patterns are produced by: 1) an initial concordant dispersal that establishes what much later may be recognized as a generalized track; 2) followed by the development of geographic or climatic barriers that fragment the original biotas into component parts (component nodes); 3) the vicariance events produced by barrier formation allow for differentiation

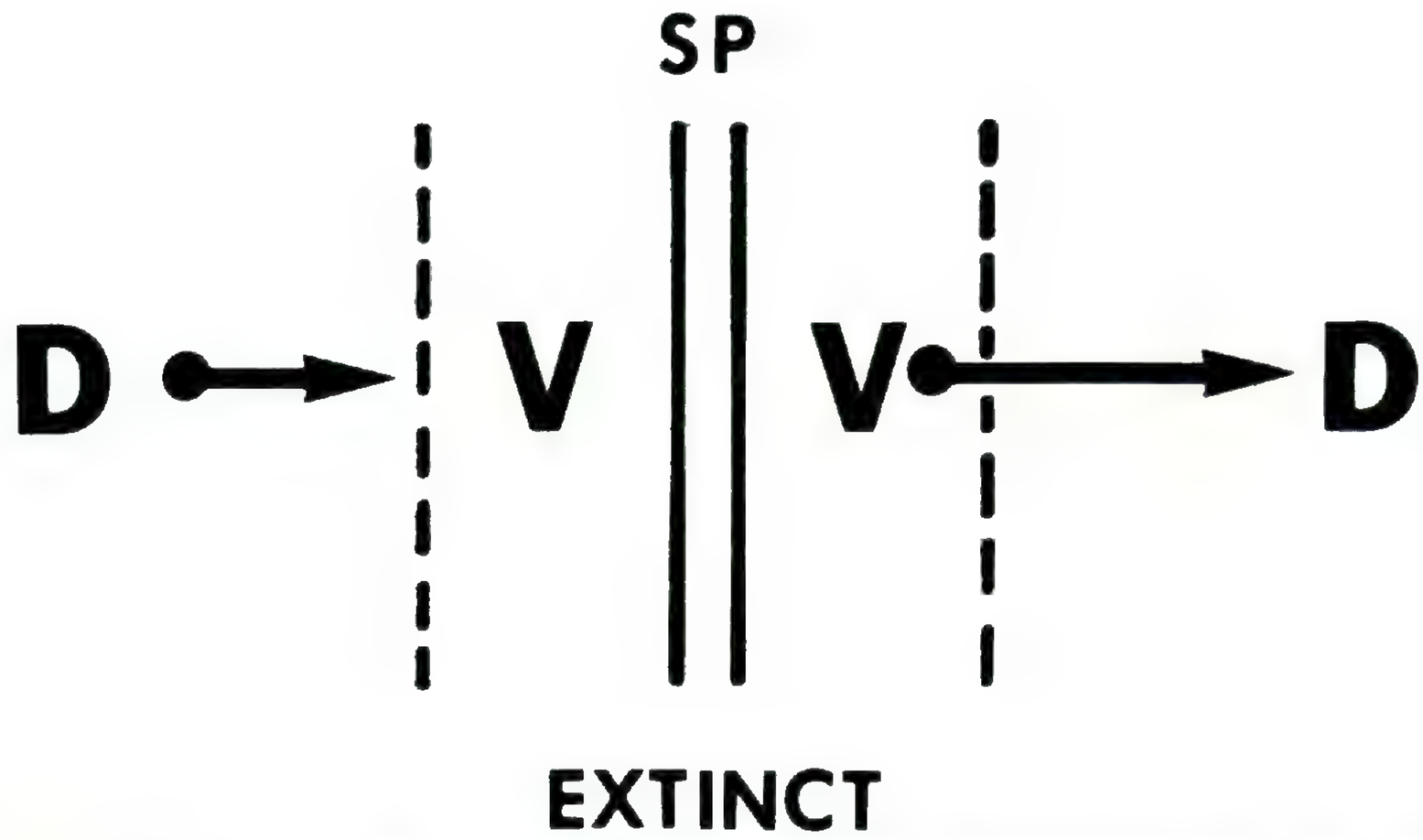


FIGURE 26. The biogeographic cycle: pattern produced through interaction of concordant dispersal (D), vicariance (V), differential differentiation (SP), and differential extinction (D). Dotted lines indicate barriers that arose after first dispersal (left) or became ineffective (right) to allow second dispersal. Solid lines represent a continuing barrier that fragmented original stock into two.

of the components; 4) with time, endemic vicariant biotas are formed and their composition becomes molded by differential rates of evolution (initially by speciation) and by differential extinction; and 5) when the barriers are removed or loosened, concordant dispersal will occur again.

While cladistic analyses of phylogenetic-area relationships may provide substantial insight into biogeographic history, the effects of differential rates of evolution, differential extinctions, and subsequent dispersal will cloud the underlying sharpness of pattern produced by the key vicariance events. A final factor that reduces refinement of the pattern is that of time. Ancient patterns can only be ascertained from ancient groups; more recently evolved lineages will have their patterns correlated with more recent events in earth history.

In terms of Central American biogeography, each of the pattern-producing processes summarized above may be recognized: Dispersal I and II from South America and North America, respectively; Vicariance I and II to isolate the Middle American area and its northern and southern derived components; differentiation of the latter *in situ* while vicariant relatives in South America and eastern North America also underwent differentiation and differential extinction; and finally, Dispersal III from South America across the Isthmian Link from early Pliocene onward. In addition, as predicted, the patterns for those ancient major groups, angiosperms, fishes, amphibians, and reptiles (well-differentiated in Mesozoic), confirm the biogeographic history for Cretaceous to Recent. On the other hand, placental mammals (and probably birds), which did not undergo differentiation until into Tertiary times, reveal only the later elements of the story.

The biogeography of the Central American region is now understood in broad outlines.

The processes responsible for its development, the interplay between earth and climatic history and the concordant dispersal and subsequent vicariance of its biota, modified by differential rates of evolution and extinction and the time

of differentiation of major taxa, are also recognizable and may be tested by future cladistic analyses of interrelationship. It seems almost trite to state that this report concurs with the single major tenet of dispersal *and* vicariance biogeography, that the former process produces widespread biotas, which are subsequently fragmented by the latter process into the highly subdivided fractions seen today.

One problem remains, the nature of the geologic event that produced Dispersal I, which, when followed by Vicariance I (obviously, the formation of a marine barrier in the Panamanian region) led to the observed differentiation of Middle American from South American units. Everything in the biotic history of Central America, except the too recently differentiated mammals, demands a land connection or its equivalent, a series of closely proximate islands between Central and South America in late Cretaceous-Paleocene. Geologic evidence for such a connection is absent or ambiguous, as discussed above. Still, it seems that if the tenets of scientific biogeography are sound, then biotic data can predict previously unrecognized geologic patterns. In essence, when in doubt, it is best to let the biota tell one what has occurred. If it is agreed that the fossil record is incomplete, then fossils cannot decisively contradict evidence from Recent distributions (Patterson, 1981) and it follows that if the geologic record is inconclusive, or ambiguous, it cannot contradict the evidence from Recent and past distributions. While it remains tempting to support the argument for the presence of the Cretaceous-Paleocene land connection by manipulating conflicting geologic evidence, especially that from the expanding earth school (Owen, 1976; Carey, 1976; Shields, 1979), I eschew any further attempt to locate the proposed structure. The organisms speak for themselves. Their distributions require the presence of a late Cretaceous-Paleocene intercontinental connection to explain the interrelationships of the biotas of Central and South America and the Greater Antilles (Fig. 24). The biological evidence stands as a challenge to geologists and other biogeographers who doubtless will wish to invalidate the hypothesis. If they undertake that task, it is incumbent upon them to provide a better explanation than mine, based upon a full evaluation of the evidence. I remain convinced that further studies will only enhance the explanatory power of the proposed model and will ultimately confirm the reality of the predicted early intercontinental connection. Hopefully, this challenge will stimulate a resurgence of interest in the biology and geology of the Central American region and that resurgence may lead to a concrete solution of the problem. Until then, I rest my case!

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THE ORIGIN OF THE PTERIDOPHYTE FLORA OF CENTRAL AMERICA

LUIS D. GÓMEZ P.[1]

The biogeographical relationships among the Central American pteridophytes were first suggsted by Hermann Christ in his introduction to the ferns and fern-allies in *Primitiae Florae Costaricensis* (Bommer & Christ, 1896). Christ distinctly identified among his collections those elements considered by him to be of Mexican origin and those he thought best represented the South American vegetation.

In his Geographie der Farne, Christ (1910) published his interpretation of the Central American fern flora, mostly based on the ideas of Carl Werckle (1909), with whom Christ corresponded, and who identified a Mesoamerican vegetational type as quite different from both the true Mexican and the South American counterparts. Winkler (1938) augmented Christ's dicta with the addition of many new records.

Recently, Tryon (1972) published on the geographical distribution of the continental pteridophytes and defined Central America as one of his regional centers (Fig. 1), based on the evaluation of some 400 taxonomic units extracted from floras, monographs and herbaria. In 1975, Lellinger proposed a phytogeographical analysis of the Chocó vascular cryptogam flora, which resembles that of the Costa Rican and Panamanian floras. Both Tryon and Lellinger rely heavily on the comparison of lists of species, a method which, in my opinion, can only partly reflect the vegetational history of an area.

Rather than repeating their comparative researches and thus reaching similar results, I intend to outline the processes by which Central America has become one of the richest and most complex floristic areas of the world. I begin with the following two premises: a) the Pteridophyta is a very ancient group of plants that probably originated in tropical environments; b) because of geological events, Central America can be divided into an older, northern portion known as Nuclear Central America (Vinson & Brineman, 1963) and a southern, younger territory that comprises the southern parts of Nicaragua, all of Costa Rica, and much of Panama. I believe the first statement will require no further explanation, and the second has had an excellent exposition by Dr. Coney (this symposium, also see Weyl, 1980). Tryon (1972) presented sufficient evidence of the strong affinities between the current Mexican, Central American, and South American floras. I only would like to challenge some of his interpretations, particularly those concerning his definition of "centers for speciation" and his conclusions regarding long range dispersal in such generalized terms.

CONTINENTAL DRIFT

The land masses of North and South America acquired their stock of pteridophytes during the Carboniferous, when the continents shared a common flora.

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[1] Herbario Nacional de Costa Rica, Museo Nacional, P.O. Box 749, San José, Costa Rica.

ANN. MISSOURI BOT. GARD. 69: 548–556. 1982.
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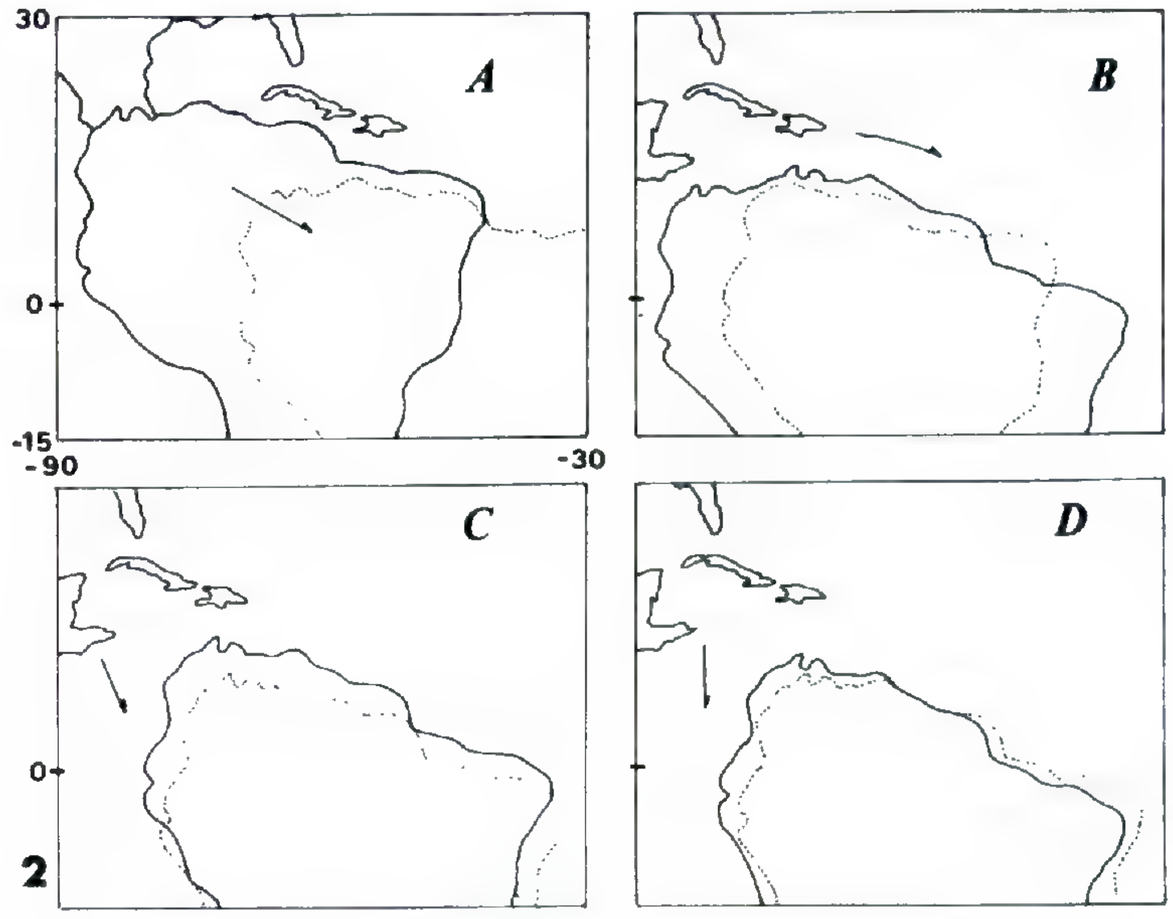


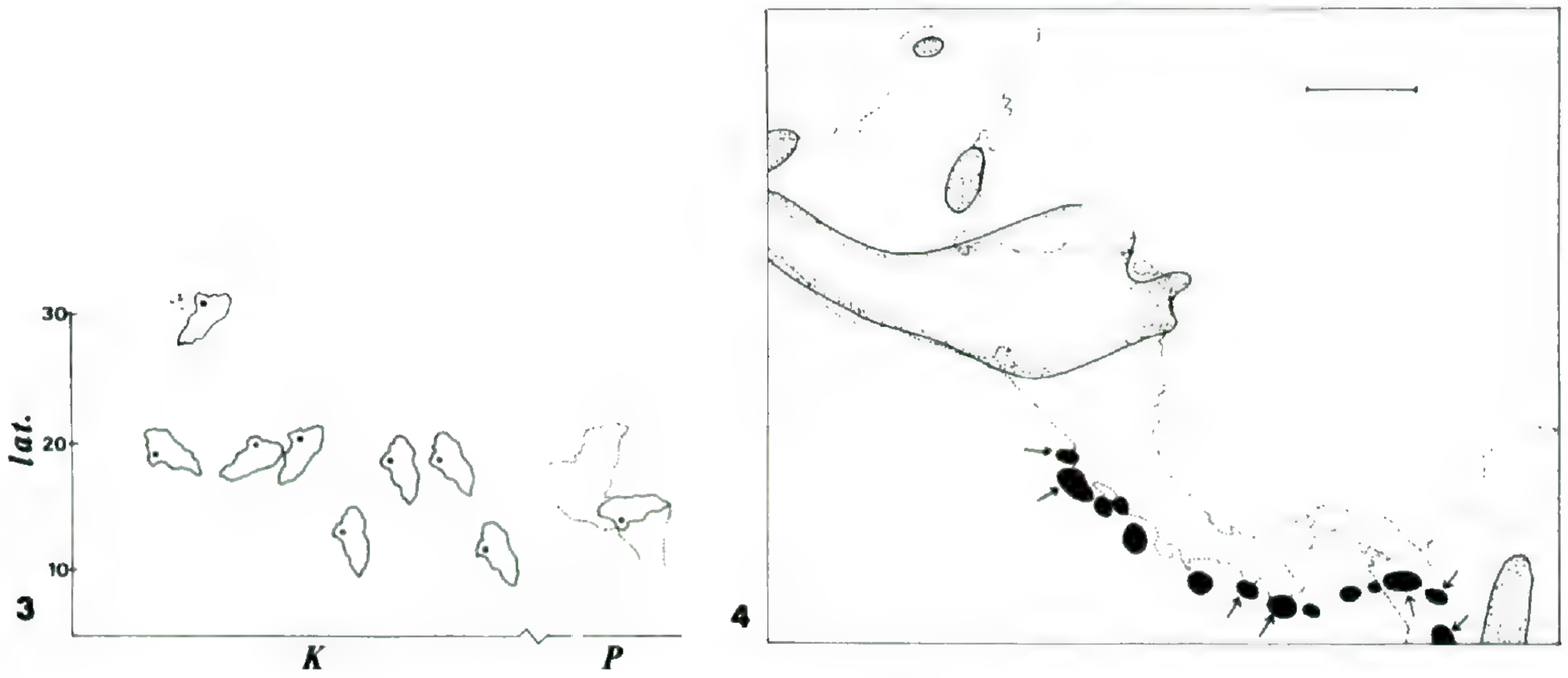
FIGURES 1–2.—1. Tryon's (1972) regional centers of continental tropical American ferns: 1—Mexican, 2—Central America, 3—Andean, 4—Guyanan, 5—Brazilian. All except 2, 4 considered as primary centers.—2. Relative motion of South America from Early Jurassic to Late Tertiary. a) Hettangian-Valanginian (180–127 m.y. B.P.), b) Valanginian-Coniacean (127–84 m.y. B.P.), c) Santonian-Eocene (84–38 m.y. B.P.), d) Oligocene-Miocene (38–0 m.y. B.P.).

Fossil records attest to intercontinental plant migrations under more or less homogeneously tropical and subtropical climates (e.g., fossilized remains of palms, cycads, and tropical ferns in areas now in the Arctic and Antarctic). At the turn of the Upper Carboniferous, the continents had drifted well apart and those ancient groups began their speciation and adaptation through isolation, giving place to disjunctions and extinctions as well as to some pantropical distributions. For example, Cyatheaceae are well distributed; Loxsomaceae are disjuncts between New Zealand, Bolivia, and Costa Rica; Matoniaceae are at present found only in the Old World tropics but were once common in Mexico and Colombia (Tomasini, 1981; van der Hammen, 1961a).

In the New World, continental drift not only separated Central America from the palaeotropics but also caused a north to south movement of the north and south cratons (Fig. 2), each portion carrying an ancestral stock of the same flora. Some of the present day interpretations of long range dispersal may be just the results of such partitioning and migration of the continental land masses, for instance, in the heterosporic fern-allies such as the *Selaginella rupestris* group, *Isoëtes mexicana-gardneriana* group, some lycopods, and some ferns.

During this time of southward migration, emergent lands were subjected to a succession of relatively rapid environmental changes related to latitudinal displacement (Fig. 3) resulting in speciation through adaptation and in expansion of the flora depending on their proximity to larger land masses. In Honduras, the fossiliferous beds show a remarkable array of plant groups that denounce climatic variability and floristic influences, particularly in the San Juancillo coal layers.

By various processes, the northern geosyncline filled up with materials from the North American craton bringing the southern limit of Nuclear Central America much further south than usually thought, the only aspect in which I do not agree with Dr. Coney, as I place that limit somewhere in the middle of Nicaragua



FIGURES 3–4.—3. The position of Honduras during part of the Cretaceous (K) relative to its present position (P). The dot marks a geographical point.—4. Palaeogeography of the Upper Cretaceous. Lines indicate the emerged lands. Solid areas represent volcanic islands, the arrows point to those still extant.

just north of the Lake Nicaragua, more or less coinciding with the natural austral limit of the genus *Pinus*. Likewise, the Andean geosyncline augmented the already rising volcanic edifices in the area now occupied by Colombia. In the Middle to Upper Cretaceous, the gap between the North and South American continents was beginning to diminish (Fig. 4).

CENTRAL AMERICA, ISTHMUS AND LAND BRIDGE

By the Miocene, both the north and south continents had reached their present positions and had had enough time, if time be needed, for their floras to speciate

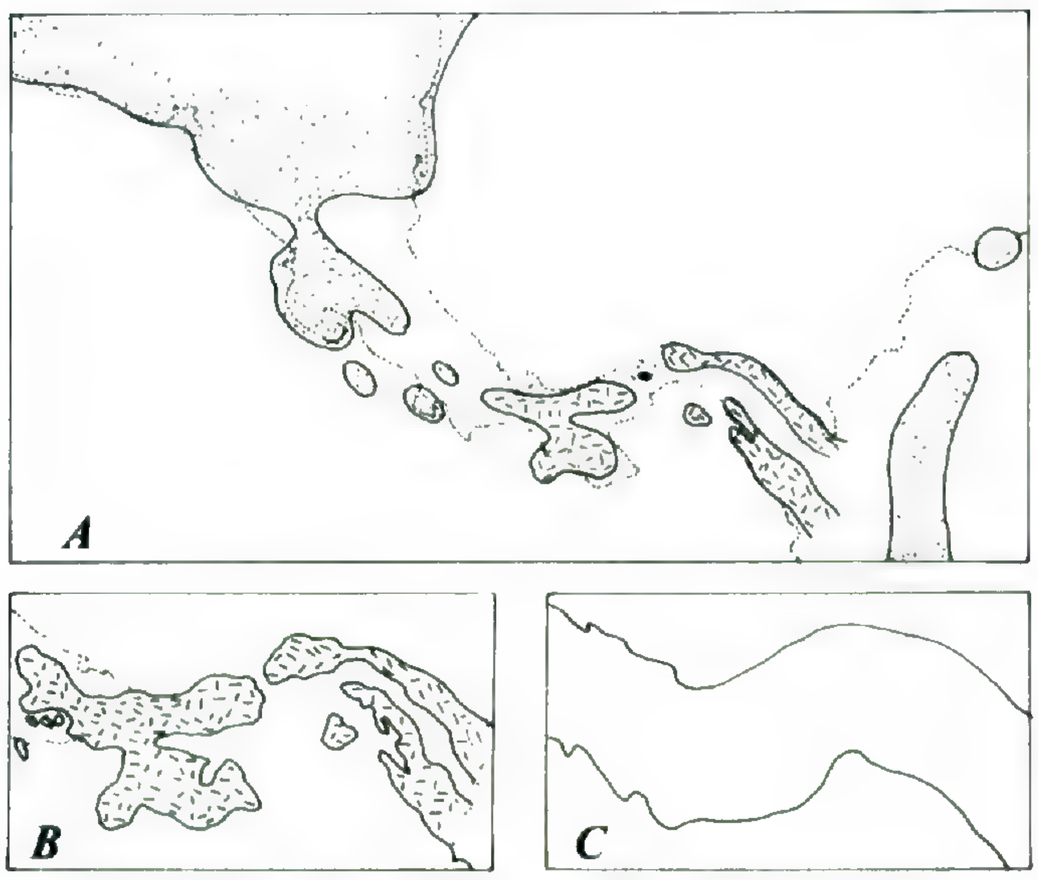


FIGURE 5. Palaeogeography of southern Central America from the Upper Oligocene to the Lower Miocene. Dotted areas indicate emergent lands. Broken lines indicate deposits of volcanic rocks, submarine or emergent.—B. Panama during the Upper Oligocene, emergent areas consisted of volcanic sediments.—C. Panama during the last marine regression of the Quaternary. The land bridge is by then completed and without gaps.

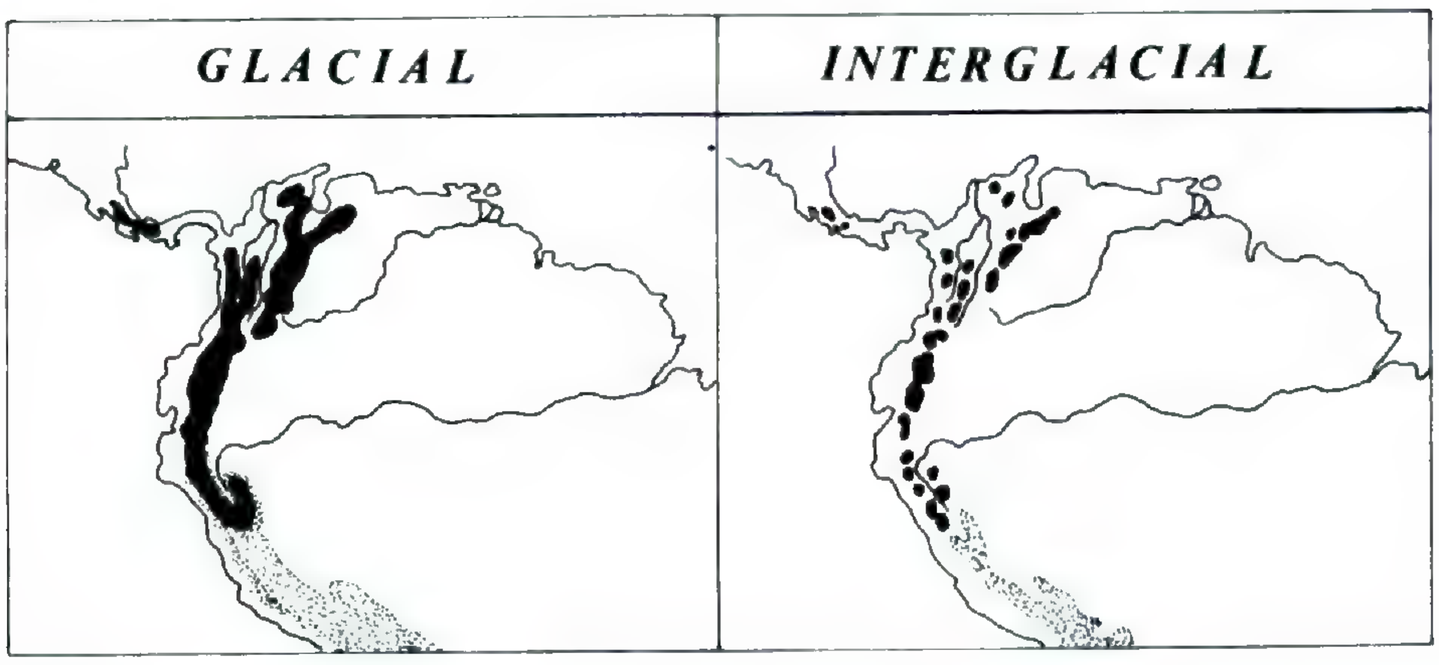


FIGURE 6. Distribution of paramos and punas during and after the last glaciation. Solid areas represent paramo, dotted areas are the punas (taken from Vuilleumier, 1981, modified).

and evolve enough to become distinctively the North American-Mexican elements, the Greater Caribbean element, and the South American element, the latter subdivided both geographically and climatically into Amazonian, Andean, and Patagonian. Those parts of North and South America that remained within the Tropics developed a rich pteridophyte flora both by geographic isolation and peripheral speciation.

The geosynclinal phenomena, coupled with intense volcanic activity and the interactions of the Cocos and Caribbean Plates, started the outcropping of the Central American isthmus south of middle Nicaragua and north of Colombia in a fast succession of events (Fig. 5), which produced the final land bridge between North and South America. This bridge was the stage of one of the greatest migratory phenomena of all ages, permitting the north-south-north passage of flora and fauna well known to us all (Simpson, 1980).

It is at this stage that it is necessary to look, albeit briefly, into the Caribbean-Central America relationship, which corresponds to two different geological causes, that of Continental Drift and plate tectonics for the Greater Antilles, and Late Tertiary volcanic phenomena for the Lesser Antilles. The floristic links between those Caribbean islands and Central America has been studied and documented for the Angiosperms elsewhere (Howard, 1973), and partially for the ferns by Tryon (1972). Few pteridophytes, other than cosmopolitan species, are shared by Antilles and Central America, *Adenoderris, Fadyenia, Neurodium,* some species of *Anemia* and *Lygodium,* the *Selaginella pallescens-harrisii* complex, species of *Botrychium* (e.g., *B. jenmanii, B. alabamensis* complex), *Lycopodium serratum,* etc., all serve as examples of Mexican-Caribbean-Central American exchanges. The rise of the Lesser Antilles by a series of volcanic events resulted in a bridge from northeast South America to Yucatan via the Greater Antilles, thus influencing circumcaribbean migrations under mediterranean conditions (Kruckow, 1980).

CLIMATIC INFLUENCES

The drastic climatic changes that took place during the Pleistocene greatly influenced massive migrations through the already completed and available Central American land bridge (van der Hammen, 1961b). There is no reason to ex-

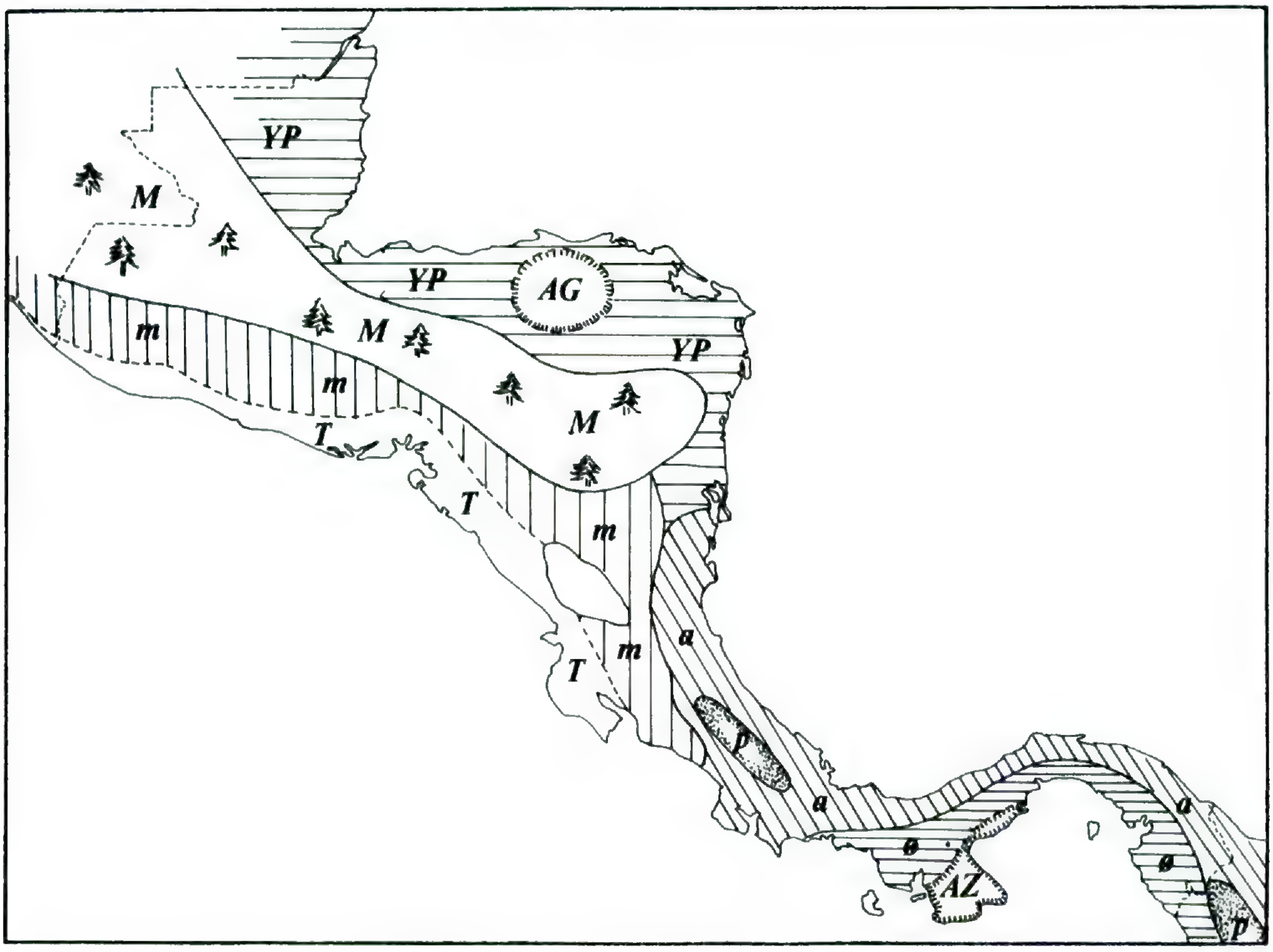


FIGURE 7. Vegetational types of Central America. T—The Tehuantepec xeric-sub arid vegetation; M—Mexican central highland elements, delimited by natural distribution of *Pinus*; m—Mexican mid-elevation elements; YP—the Yucatan/Peten flora; a—amazonian; ø—mixed Pacific South America and Amazonian; p—South American paramos or Andean elements. AG—the dry Pacific related flora of the Aguan valley in Honduras. AZ—Azuero in Panama is more closely related to the Venezuelan Llanos and northern South American savannas of the eastern coast.

clude vegetation from such migratory movements toward more favorable climates, if the latter are understood as more or less homogeneous higher temperatures and evenly distributed higher rainfall, such a favorable climate was prevalent in the Isthmus, which was and still is climatically moderated by two ocean fronts.

Glaciation proved important inasmuch as it affected the higher mountain ranges, creating the environmental conditions propitious to the migration and establishment of Andean elements, as well as some temperate, northern migrants, in what is a classical example of the compensatory effect of altitudes instead of higher latitudes. For example, the core analyses of Martin (1960) indicated that paramo-type vegetation existed in Costa Rica more or less 600 m below its present limits. This undated finding was further corroborated by Vuilleumier (1981; Fig. 6), whose findings apply also to ferns, such as: *Lycopodium saururus, L. brevifolium, Jamesonia* spp., and *Eriosorus* spp., found mixed with northern pteridophyta, e.g., *Hypolepis, Polystichum,* and *Odontosoria,* all Mexican elements, and even with some nearctic ones (*Asplenium monanthes, Cystopteris fragilis, Pellaea* spp., etc.).

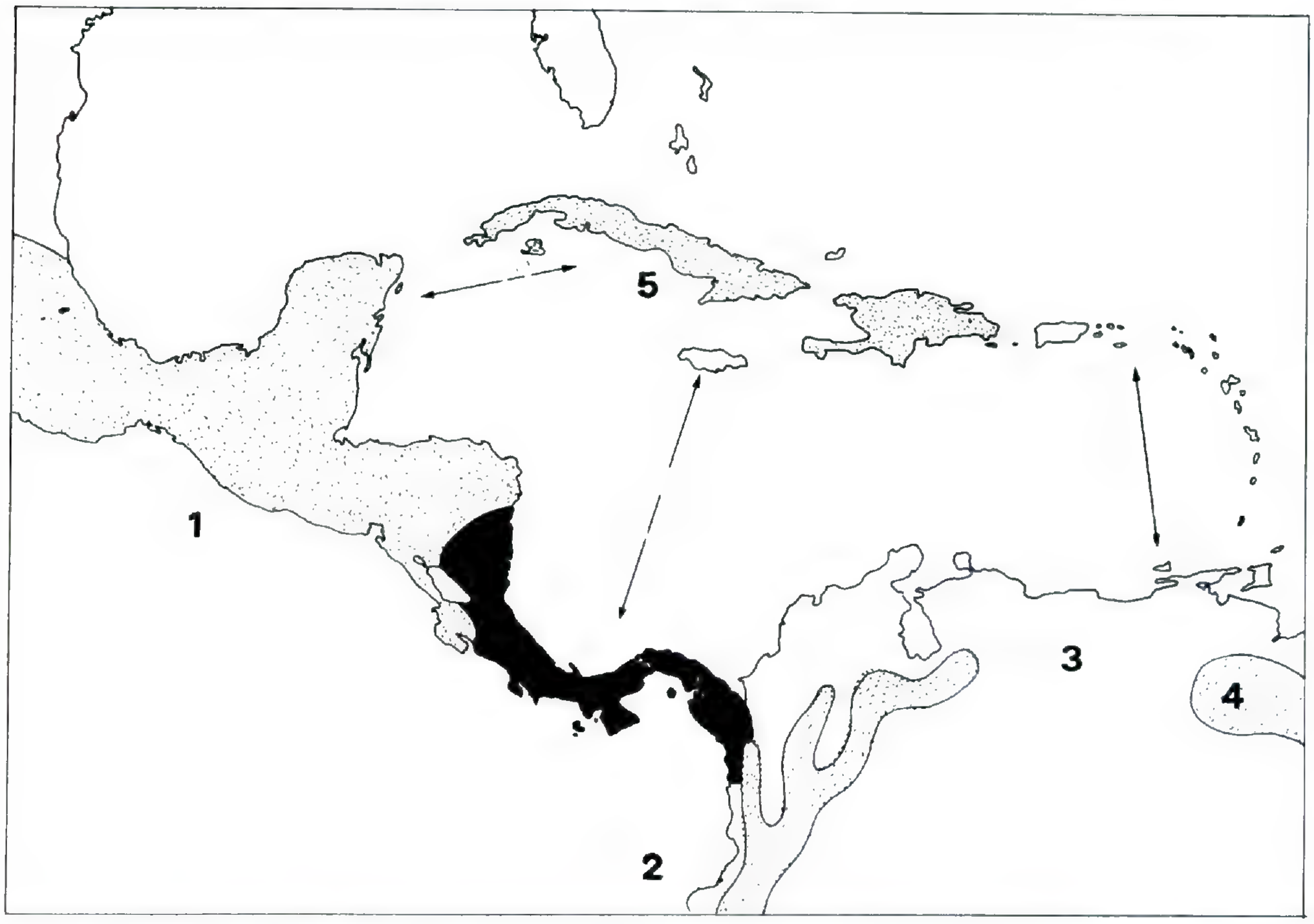


FIGURE 8. The pteridophyte flora of Central America is composed of 1—Mexican-Nuclear Central American elements, 2—Andean, 3—Amazonian, and 5—Antillean. The Guyanan element, 4, is not significant. The solid area indicates higher endemism in the area and the greatest diversity of species per area unit. Arrows indicate areas of greater affinities.

VEGETATION TYPES

Because of its complex geological and climatic history, the Central American Isthmus has been invaded and populated by a series of floristic contingents both from the North and South continental land masses. These vegetations have moved and adopted distributions determined, among many other factors, primarily by edaphic types, rainfall, and altitude. Figure 7 illustrates my concepts of floristic influences, unlike several other vegetation maps, which only detail physiognomic characteristics of the plant cover (Trejos & Archer, 1953; Holdridge, 1957; Lauer, 1960). The proposed eight vegetational elements (Gómez, 1982) are in agreement with the relationships other authors have suggested for various Central American, Mexican and Northern South American localities (Bartlett & Barghoorn, 1973; Beard, 1944, 1953; Breedlove, 1973; Carlson, 1954; Cuatrecasas, 1957; Lundell, 1937; Standley, 1938; Wagner, 1964; Weber, 1958; Werckle, 1909; Williams, 1938). In the eight vegetational zones, the pteridophytes found are those typically associated with or recorded from the parental areas or centers of distribution, with mixed floras occurring along the transitional, bordering lines.

DISJUNCTS

When the flora of a given area is well known, it is easy to spot those organisms that are disjunctive in their distribution. Wagner (1972) has presented and doc-

umented the importance of disjunctions in the Pteridophyta of the United States. But neither the Central American floras nor those of immediate neighbouring areas are well known and any interpretation here would run the risk of being potentially misleading. For example, I reported (Gómez, 1973) the presence in Costa Rica of several Mexican ferns, e.g., *Cheiloplecton, Schaffneria,* thought to be endemic to Mexican highlands and subarid areas. The former I have recently collected in Nicaragua and the latter is reported by Stolze (1981) from Guatemala. *Woodwardia* was reported for Costa Rica (Gómez, 1972) as a 1,000-mile disjunct from the nearest Mexican population but it is now known from Guatemala, Honduras, and northern Nicaragua.

There is one spectacular case, that of *Loxsomopsis costaricensis,* an endemic fern with its only other confamiliar in New Zealand. There are no geological indications that Costa Rica and New Zealand were ever connected, not even in the most fertile imagination. Could this case be an indication of a need to review Copeland's (1940) mind-twisting idea of the Antarctic origin of tropical ferns?

The point I am trying to make is that to talk about disjunctions one needs to be certain that there are no intermediate populations of a species between the known and the newly discovered locality.

LONG RANGE DISPERSAL

The preceding lines lead me into a delicate subject I preferred to ignore during the actual presentation of these notes. Professor H. Iltis addressed the one million dollar question by asking What, if not long range dispersal, can explain the distribution of organisms, namely the ferns? I declined to answer then for two reasons: a) the possibility of an ensuing battle between the more or less even numbers of "vicars" vs. "old timers," and b) because the question of long range dispersal would require a symposium of its own and, at that moment, many more minutes at the podium, in itself a horrid prospect . . . .

I do not discard long range dispersal as an effective method of distribution. I do think it is *one* very good way to move about. If I were to reject it, the African bees, Man and other beasts would prove me wrong. But, if that were the only mechanism involved for the air-borne fern spores, I yet have to find clumps of *Matonia, Dipteris, Stromatopteris,* etc., all Old World tropical ferns, growing in my backyard to become a blind adept of this theory. Certainly, the environment itself could never be so selective of those colonizers which readily grow adventitiously around our greenhouses. Even if it were so highly selective there would be problems, such as the one posed by root-parasites and their specific hosts. *Balanophora fungosa* in the Pacific basin and *Prosopanche costaricensis* in Costa Rican rainforests, serve as examples.

Then, what about heterosporous pteridophytes? I find the explanation of *Selaginella peruviana* in southwestern United States and the Peruvian Andes in continental drift and vicariance rather than in long range random dispersal. The many cases of amphipacific, amphiatlantic, and circumboreal disjunctions cannot be explained solely on the basis of continental drift or long range dispersal. In this particular item, what is good for the goose may not be at all good for the gander and scientists have to be careful not to fall prey to excessive fadisms.

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NEOTROPICAL FLORISTIC DIVERSITY: PHYTOGEOGRAPHICAL CONNECTIONS BETWEEN CENTRAL AND SOUTH AMERICA, PLEISTOCENE CLIMATIC FLUCTUATIONS, OR AN ACCIDENT OF THE ANDEAN OROGENY?[1,2]

ALWYN H. GENTRY[3]

The interchange of plant species between North and South America has been a major factor in determining the Neotropical phytogeographical patterns observed today. Although this has long been realized, recent historical geological evidence as well as increasing knowledge of today's distributional patterns now makes possible a more thorough analysis of how these patterns originated. This paper briefly reviews the geological background, summarizes the composition of the extant Neotropical flora, points out the striking ecological consistency of many taxa and life forms, and suggests how some of the present phytogeographical patterns have developed from the interplay of these factors.

GEOLOGICAL BACKGROUND

Several major geological events have had profound effects on the evolution and distribution of the Latin American flora. One of the most significant of these was the separation of South America from Africa that began only 127 million years BP (Rabinowitz, 1976; McKenna, 1981) with contact or near-contact present until 80–90 million years BP (Raven & Axelrod, 1974; McKenna, 1981). During most of the first third of angiosperm evolution, a time during which many of the modern orders and families of plants arose, South America was a part of the West Gondwanaland cradle of the angiosperms (Raven & Axelrod, 1974). However, during virtually all of the Tertiary and much of the Cretaceous South America was an island continent, at least from the perspective of tropical plants, and most of the evolution of its rich and varied flora took place in isolation following separation from Africa. Thus, such characteristic and ecologically important trop-

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[1] This paper was presented in both Symposia published in this issue of the Annals of the Missouri Botanical Garden—the Symposium on Plant Geographical Results of Changing Cenozoic Barriers at the XIII International Botanical Congress in Sydney, Australia, 1981; and the 1981 Systematics Symposium of the Missouri Botanical Garden. As used herein, references documented as "this symposium" include papers from both symposia.

[2] This paper stems largely from insights developed during field work over a number of years in various parts of Latin America, and supported by the National Science Foundation (GB 40103, INT-7920783, DEB-8006253, DEB-UT-20325, DEB-8006253), the National Geographic Society, and USAID (DAN-5542-G-SS-1086-00). I thank P. Ashton, D. Axelrod, C. Dodson, A. Graham, P. Raven, J. Rzedowski, J. Terborgh, and B. Simpson for reviewing the manuscript and numerous colleagues including D. Austin, H. Balslev, C. Berg, W. Burger, L. Constance, G. Davidse, R. Faden, P. Fryxell, S. Graham, R. Haynes, M. Huft, N. Holmgren, M. Johnston, J. Kuijt, J. Luteyn, M. McKenna, W. Meijer, J. O'Neill, R. Bleiweiss, T. Plowman, M. Poston, J. Pringle, H. Sleumer, L. B. Smith, D. Soejarto, C. Stace, P. Taylor, W. Wagner, D. Wasshausen, H. Wilson, and D. Wunderlin for providing data on Neotropical species numbers or distribution patterns of their taxonomic specialties.

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ical American angiosperm families as Bromeliaceae, Humiriaceae, Cactaceae, and Caryocaraceae, had ample time to evolve and radiate in South America.

Although the history of the separation of South America from Africa is clear, the tectonics of the earlier separation of North America from the Gondwanan land mass is still uncertain (see Coney, this symposium). Apparently North America (including the Central American peninsula) separated from Africa-South America in Jurassic time, well before the origin of the angiosperms (Lillegraven et al., 1979). However, by late Cretaceous a chain of volcanic islands (Nicoya Complex) had developed connecting Central America with Ecuador (Dengo, 1975; Lillegraven et al., 1979). New geological evidence (Dickinson & Coney, 1980) suggests that a connection between nuclear Central America and South America was reestablished in Late Cretaceous as both major American land masses moved westward more or less in tandem.

How much of the late Cretaceous connection between Central and South America was above sea level is not known, although it probably consisted mostly of an interrupted island arc. Further complicating the picture, much of northwestern South America was submerged during most of the Cretaceous (Irving, 1975). Both the low coastal range of western Colombia and southern Darien and the northern Andean Cordillera Occidental were originally island arcs associated with westward movement of the South American plate during upper Mesozoic time (Zeil, 1979: 193). McKenna (1981) has suggested that the present Pacific coast of northern South America may have resulted from accretion during the early Tertiary of left-behind fragments of the south end of the Central American volcanic arc. According to McKenna (1981) some of the islands of this arc may have remained above water, separated from North America only by sequential opening and closing of water gaps, until colliding with South America and providing a plausible scenario for "Noah's Arc" dispersal of hystricognath rodents between North and South America, a model consistent with the discovery by Juteau et al. (1977) that much of the west coast of Ecuador is formed from a block of originally oceanic crust.

There was a general regression of epicontinental seas from northwestern South America at the end of the Cretaceous (Harrington, 1962; Lillegraven et al., 1979) concomitant with a late Cretaceous orogeny that gave rise to the forerunner of the Colombian Cordillera Occidental (Irving, 1975). More than 160 km was added to the northwestern South American continental margin during Late Cretaceous time. The Greater Antilles, then far to the south of their present position and in part submerged, presumably also constituted part of some kind of late Cretaceous inter-American connection as suggested by Malfait and Dinkelman (1972) and discussed in the context of biogeography by Tedford (1974) and Rosen (1974). (See Pregill (1981) for a different interpretation but much of the geology on which it is based (Perfit & Heezen, 1978) has apparently been superseded (Dickinson & Coney, 1980; Coney, this symposium).) According to this interpretation, the continued westward movement of South America and the slightly southwestward movement of North America led to decoupling faults that separated the proto-Antilles from both land masses. A new subduction zone then formed to their northeast as the proto-Antilles moved northeastward. Continued westward movement of South America and southwestward movement of North America led to

pinching off of a segment of the Pacific plate as the Caribbean plate, with relatively eastward displacement of the whole Caribbean region relative to South America. Probably nuclear Central America south of the Motagua fault also moved eastward with the Caribbean plate from an original position more directly south of Mexico, closing part of the gap between North and South America (Dickinson & Coney, 1980). In the late Teritary, formation of the Central American trench and an associated new epoch of volcanism again led to uplift of islands in the region between South America and nuclear Central America. These islands eventually coalesced into today's lower Central America with substantial land connection across the Isthmus of Panama established in the Pliocene apparently only about 3 million years ago (Keigwin, 1978; Marshall et al., 1982).

Although closing of the Isthmus of Panama between North and South America was clearly one of the most important "changing Cenozoic barriers" for the Latin American biota, the presence of a previous, albeit interrupted, late Cretaceous connection would have provided shorter water gaps between the continents fairly early and thus may modify our concept of the phytogeographical importance of this late event. In late Cretaceous time many modern families and genera of plants were extant in West Gondwanaland and in a position to take advantage of island stepping-stones between South and North America.

Thus most of the cases of exclusively or predominantly American families like Cactaceae with strongly differentiated components in both tropical North and South America, which Raven and Axelrod (1974) accounted for by chance relatively long distance dispersal at various times during the early Cenozoic, may reflect instead more or less direct late Cretaceous migration between the two continents, presumably mostly via island hopping. Similarly, the dichotomous composition of the West Indian flora, with both strong southern and northern affinities, would be expected as the result of an original stocking of a proto-Antillean region located between North and South America as emphasized by Rosen (1974), although his arguments for direct land connections do not accord with the geological evidence (Coney, this symposium). This dichotomy may have been even stronger in the early Tertiary to judge from the presence of now locally extinct otherwise exclusively South American taxa like *Aetanthus* (although there may be identification problems in separating this from the generalized northern *Loranthus* pollen type that was already present in Europe in the Eocene, according to Muller, 1981) and *Catostemma* in the Oligocene of Puerto Rico (Graham & Jarzen, 1969) along with northern elements like *Fagus, Hauya, Engelhardtia, Liquidambar,* and *Nyssa,* which have never been able to reach South America.

That the interrupted link between North and South America was completely ruptured at the beginning of the Tertiary, as the proto-Antilles began their northward movement, means that only those very old taxa already extant in the Cretaceous would have had the opportunity for more or less direct inter-American island hopping prior to the Pliocene formation of the Isthmus of Panama. In general, the flora of the early Tertiary of what is now temperate North America seems to have been more like the modern tropical American flora than it is today. However, it is very difficult to judge to what extent the apparent affinities of Paleocene and early Eocene North American and South American floras might

represent shared descent from hypothetical common wide-ranging middle Cretaceous early angiosperm stocks, or whether they suggest an independent, relatively direct floristic interchange between South America and tropical North America subsequent to the separation of Africa and South America. The difficulty of floristic interpretation is compounded by the serious taxonomic errors in identification of fossil floras that are now known to have characterized much early paleobotanical work (cf. Graham, 1972: 8; Dilcher, 1974; Hickey & Wolfe, 1975). As summarized by Leopold and MacGinitie (1972), the floristic affinities of the Rocky Mountain region, the only part of then biotically tripartite North America in potentially direct contact with nuclear Central America, show successive changes through the early Tertiary. They find the generalized Paleocene flora difficult to relate to that of any extant phytogeographic region, but suggest that the mesic early Eocene flora was primarily related to the southeast Asian subtropical and warm-temperate mixed mesophytic forest, the middle and late Eocene floras to those of the subhumid Central American tropics, the Oligocene flora to the live oak forests of the highlands of northern Mexico, and a final shift to modern Cordilleran conifer forests in the Miocene (Leopold & MacGinitie, 1972). Presumably most of the genera shared with South America during the latest Cretaceous and earliest Tertiary reflect wide-ranging Cretaceous common ancestors (cf. Raven & Axelrod, 1974), while the subhumid middle and late Eocene flora analyzed as characteristically and autochthonously tropical American in origin would have to represent either an old uniquely tropical North American flora (which later must have spread to South America to account for the overwhelmingly pan-American distributions of most of those genera today) or early floristic interchange with South America. Contrary to the Central American[4] distributional centers suggested for such genera as *Ocotea*, *Beilschmiedia*, *Cedrela*, *Luehea*, *Oreopanax*, and *Swartzia* by Leopold and MacGinitie (1972), all are better represented today in South America than in Central America with the possible exception of *Cedrela* (three of the eight species only in Central America, and two others also occurring there). Even three of the four genera—*Homalium*, *Bernoullia*, *Beilschmiedia*, and *Engelhardtia*—related to Rocky Mountain fossil forms and suggested as endemic to Central America in their American ranges, are as well or better represented in South America. Unfortunately the Tertiary fossil record from Central America and South America is inadequate to show when such genera achieved their modern pan-neotropical distributions, but phytogeographic and ecological evidence suggests that it was long before establishment of the Panamanian land bridge. Many of these plants have wind-dispersed or mammal-dispersed seeds or fruits and are unlikely candidates for long distance dispersal (Gentry, 1982a), which would be consistent with having achieved their present distributions via a relatively direct inter-American migration route, presumably prior to the Eocene.

Although some South American floristic elements evidently reached Central America early, perhaps via island hopping along the late Cretaceous Antillean connection, the Tertiary floras of South America and North America remained

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[4] Central America is used throughout this paper in a broad sense to include Mexico.

fundamentally different (Germeraad et al., 1968). For example Graham's (1973, 1982) analysis of the Paraje Solo formation suggests that in the Miocene the southern Veracruz lowlands had only a few scattered representatives of the South American-derived tropical forest which now characterizes the region, while a basically North American plant community, similar to the deciduous forest of the eastern United States and today restricted to intermediate elevations, was well represented. Pollen of ten of the fourteen arborescent genera that would have been expected in similar deposits in the southeastern United States is present. While redeposition of pollen from plants growing at higher altitudes could have affected these results (Axelrod, pers. comm.), it is clear that the eastern deciduous forest elements were at least present in the region. In contrast, the Paleocene pollen flora of Colombia contained exclusively such lowland tropical elements as Annonaceae, Bombacaceae, Melastomataceae, Araceae, and several genera of palms: *Mauritia, Astrocaryum,* and several pollen genera (Hammen & Garcia, 1966).

Further south in Central America, in then recently emerged Panama, only three of the temperate North American genera—*Alnus, Juglans,* and *Myrica*—are present in the Miocene Gatun formation and none of them are present in earlier Panamanian deposits (Graham, 1973). These same three genera appear in the South American palynological record only subsequent to closing of the Isthmian connection in latest Pliocene and Pleistocene times. The many widespread South American families and genera that today barely enter Central America in eastern Panama provide evidence that the Tertiary barrier to northward migration was equally effective. As might be expected, none of the South American taxa that barely enter Central America are represented in the West Indies either. To summarize, the water gap between North and South America separated two very distinct Cenozoic floras in the two continents despite a probable early opportunity for relatively direct island hopping across the proto-Antillean chain. However, the opportunity for limited late Cretaceous migration between South and North America would readily account for the many characteristically Gondwanan taxa with distinctive and strongly differentiated Central American derivatives (see below).

The second Cenozoic geological event with major phytogeographical importance for the Neotropics was the uplift of the Andes. Although the Andean orogeny was certainly more complicated than often supposed (Zeil, 1979), the general picture of major uplift of the already extant southern and central Andes in the Mid-Cenozoic and of the northern Andes more recently seems well established. The Colombian Cordillera Central is older and existed already in the Cretaceous (Zeil, 1979: 109) but probably was eroded down to a low range of hills prior to the recent orogeny. Most of the uplift of the northern Andes took place only in the last five million or so years, during Pliocene and Pleistocene times (Hammen, 1974; Flenley, 1979). The Andes are unique: by far the most extensive mountain range in the world's tropics.

A third event of major phytogeographic importance was the advent of Pleistocene climatic fluctuations associated with glacial advances and retreats at higher latitudes. In the montane tropics these climatic oscillations took the form of an altitudinal lowering and compression of vegetational zones, as elegantly docu-

mented by van der Hammen (1974) and his associates from the palynological record in the Colombian Cordillera Oriental. In the lowland tropics temperature changes associated with glacial advances were minimal but changes in precipitation were pronounced. The cycles of glacial advance and retreat were associated in the tropical lowlands with alternating dry and wet periods respectively. Contrary to early suggestions (e.g., Haffer, 1970), the wet periods of the tropics were not the same as the well known pluvial periods of arid temperate and subtropical deserts that accompanied glacial advances. Instead, tropical wet periods were perhaps 180° out of phase with the temperate-subtropical pluvial periods; as if the glacial advances tied up so much of the water of the earth's normal atmospheric circulation that not enough was left for "normal" tropical rainfall. As a result of these cyclical changes in precipitation the lowland neotropical forests were periodically reduced in extent to scattered pockets, chiefly around the periphery of Amazonia during dry periods (Haffer, 1969, 1978; Simpson, 1971; Prance, 1973, this symposium; Simpson & Haffer, 1978).

The biological significance of this dynamic model, very different from the popular conception of the stable "forest primaeval," is that it provides optimal conditions for speciation, as populations of tropical forest species repeatedly fragment and recoalesce (see papers in Prance, 1982). Some problems with the Pleistocene refuge model have been noted. For example, have long-lived trees and lianas had adequate time to speciate so profusely in the relatively short time and few generations available since the beginning of the Pleistocene? Moreover the distributional patterns that have been cited as evidence for former refugia—species pairs in many unrelated taxa coming together at coincident contact zones—could also result from in situ speciation along environmental gradients. Nevertheless the Pleistocene refuge model has been widely accepted by biogeographers as a general explanation accounting for much tropical speciation. Not only did forest species successfully survive dry periods in these habitat islands, but the repeated cycles of multiple range fragmentation could potentially have multiplied their numbers. In other words, the Neotropics have many species because of the multiplicative effect of its more numerous refugia; Africa has few because it generally lacked such refugia.

FLORISTIC BACKGROUND

One of the outstanding features of the Neotropical flora is its extreme richness in species. Thus Raven's (1976) estimate for number of Neotropical plant species was 90,000, three times as high as his estimate for tropical Africa plus Madagascar and 2½ times the estimate for tropical Australasia. Prance (1977) and other authors have generally accepted Raven's estimates. Other recent, perhaps slightly higher, estimates for continental floristic diversity are available for the Palaeotropics—30,000 species for continental tropical Africa alone (Brennan, 1979) and 25,000–30,000 species for the Flora Malesiana region (Jacobs, 1974). Nevertheless it seems clear that the estimated number of plant species for the Neotropics is much higher than for the entire Palaeotropical region. Prance (pers. comm.) estimates 30,000 species for Amazonian Brazil alone and the best available estimate for Central America is 18,000 to 20,000 (Gentry, 1978) and an (overlapping) one for Mexico is 14,000 to 20,000 (Rzedowski, 1965, 1978).

While it is generally appreciated that Africa is floristically relatively depauperate (Richards, 1973; Brennan, 1979), many studying the flora of Southeast Asia (Whitmore, 1975; Ashton, 1964, 1977) have suggested that the dipterocarp forests of that region are the world's richest, citing samples of number of tree species over 10 cm dbh as evidence. Actually, Prance et al.'s (1976) recent sample of 179 tree species ≥15 cm dbh in a hectare of forest near Manaus is as diverse as most of the Southeast Asian forests. If individual Southeast Asian forests have as many or more tree species as their neotropical equivalents, can the Neotropics really have as many more species as suggested by Raven's estimates?

The available estimations of Neotropical floristic diversity are very tentative. In order to assess more accurately whether the Neotropics are really as incredibly species rich as suggested by Raven's estimates, I decided to try to count the number of species directly. First, I compiled a list of all Neotropical seed plant genera based on the available regional floras and familial monographs, supplemented by a search through the entire Missouri Botanical Garden herbarium for additional generic names from the region. Although a few small local genera were probably missed, the resulting list of over 4,200 Neotropical genera seems reasonably complete. Second, I estimated the number of Neotropical species in each genus, using recent monographs such as the Flora Neotropica series, when treatments were available, and the figures supplied by Willis's Dictionary (Airy Shaw, 1973) in most other cases. A few additional data sources on species numbers were used for some groups—Compositae were taken from Heywood et al. (1977), Leguminosae mostly from Polhill and Raven (1981), Orchidaceae from Dressler (1981), Solanaceae from D'Arcy (1979), Verbenaceae and Eriocaulaceae from Moldenke (1980), Gramineae (mostly Davidse, pers. comm.), and Bignoniaceae, Sabiaceae, and Buxaceae from my own data. The Willis figures for species numbers are directly useful only for genera restricted to the Neotropics and in the few cases where species numbers for a genus are given by geographical region. The resultant data set accounted for over 3,660 genera with almost 65,000 Neotropical species.

Unfortunately, the other 533 non-monographed non-endemic Neotropical genera include a total of 60,000 species based on the Willis figures. These genera fall into two main groups—large pantropical genera like *Piper* or *Eugenia*, or basically Laurasian herbs that range south into the montane Neotropics. About 20,000 of these species fall into pantropical genera that tend to be well represented in the Neotropics suggesting that a third to a half (i.e., 7,000–10,000) of them are Neotropical. The remaining 40,000+ species are either in cosmopolitan genera (e.g., *Ipomoea*) or are basically temperate zone genera with relatively poor Neotropical representation (e.g., *Astragalus, Draba, Carex, Gentiana*). Perhaps only 10–15% of the total species of these genera are Neotropical, implying an overall total of at least 76,000 Neotropical species.

However, there is another serious problem in compiling such an estimate. The Neotropics are generally much more poorly known floristically than other parts of the world and very many Neotropical plant species remain undescribed. In regions like the western Colombian Chocó, probably a quarter of all plant species are strictly endemic and in many groups like Araceae or Ericaceae almost none of the endemic species have been described (Gentry, 1982a). A well-documented

example comes from the Río Palenque field station in western Ecuador where, in the process of writing a local florula (Dodson & Gentry, 1978), 61 new species were discovered in a minuscule 1.7 km^2 area; subsequent collections and re-evaluation of tentatively identified problem taxa now brings the total to almost 100 species described from Río Palenque. Such figures suggest that there must be at least 10,000 undescribed neotropical plant species that would elevate the total number of neotropical seed plant species to 86,000 or more.

We may conclude that Raven's original estimate of 90,000 neotropical species was fairly accurate. That the neotropics as a whole are extraordinarily richer in plant species than other parts of the world seems established beyond any serious doubt.

The Neotropical flora generally shows very strong pantropical connections. That pantropical distributions predominate among tropical families is well known (e.g., Good, 1974). However, these phytogeographic similarities are even stronger than generally realized, especially at the generic level and especially with Africa. For example, 30% of the genera that occur at Makokou, Gabon, are also found in the Neotropics and many more African genera are more like some Neotropical genus than like other African ones (Hladik & Hallé, 1973; Gentry, in prep.). Statistical comparisons of percentages of genera in common between different tropical areas (e.g., Thorne, 1973) are especially misleading since the important genera tend to be shared while small segregate genera contribute disproportionately to the differences. The picture is also confused by taxonomic parochialism on the part of workers on different continents.

The relevant point of these pantropical floristic similarities in the context of this analysis is that the peculiarities that distinguish the present Neotropical flora have arisen despite a common floristic stock shared at least with Africa (i.e., West Gondwanaland) and to a large extent with tropical Asia as well. In this context it is almost irrelevant whether this intercontinental commonality was derived from dispersal events or continental movements. The question to be addressed here is why this shared floristic stock has given rise to so many more species in the Neotropics.

ENDEMIC FAMILIES

The greater diversity in the Neotropics results in part from a conspicuously larger and more ecologically important complement of endemic families. Even retaining traditional broad familial delimitations, there are at least 38 endemic or essentially endemic (i.e., with one or two African species, most of whose ancestors probably arrived relatively recently via long distance dispersal) Neotropical families with a total of 5,690 species (Table 1). Thirteen of these families have over 50 species as compared to only three endemic palaeotropical families with more than 50 species—Dipterocarpaceae[5] (580 spp.), Pandanaceae (700 spp.), and Nepenthaceae (68 spp.). Six essentially endemic Neotropical families have over a hundred species, and two—Bromeliaceae and Cactaceae—have about 2,000

[5] The discovery of a primitive dipterocarp in South America (Maguire & Ashton, 1977) does not change the status of the family by the definition of "essentially endemic" used here.

TABLE 1. Endemic Neotropical families (in some cases with a single African species or a single monotypic or ditypic African genus presumably recently arrived by long-distance dispersal).

1) *Tropical forest taxa**

Bromeliaceae (46 genera/2, 108 species (plus 1 sp. in Africa))
Caricaceae (3/29 (plus one ditypic African genus))
Caryocaraceae (2/24)
Cyclanthaceae (11/178)
Dialypetalanthaceae (1/1)
Duckeodendraceae (1/1)
Humiriaceae (8/46 (plus 1 sp. in Africa))
Lacistemmaceae (2/14) (included in Flacourtiaceae in Flora Neotropica)
Marcgraviaceae (4/125)
Quiinaceae (4/53)
Rapateaceae (15/79 (plus 1 monotypic African genus))
Vochysiaceae (7/182 (plus 1 ditypic African genus))
Trigoniaceae/*Trigonia* (1/24)
Bignoniaceae/Bignonieae (46/359)
Lecythidaceae/Lecythidoideae (300)

2) *Taxa of dry and/or Andean parts of South America (a few reaching North America)*

Brunelliaceae (1/51)
Calyceraceae (4/46)
Columelliaceae (1/4)
Gomortegaceae (temp.) (1/1)
Malesherbiaceae (1/27)
Myzodendraceae (temp.) (1/11)
Nolanaceae (1/18)
Tovariaceae (1/2) (included in Capparidaceae in Flora of Panama)
Tropaeolaceae (2/92)

3) *Taxa of dry parts of tropical North America*

Crossosomataceae (1/4)
Fouqueriaceae (2/8)
Garryaceae (1/18)
Lennoaceae (3/8) (1 rare species on the dry Caribbean coast of northern Colombia)
Theophrastaceae (5/110) (a few species of *Jacquinia* and *Clavija* in South America)

4) *Taxa of dry tropical/subtropical parts of both continents*

Cactaceae (62/2,000) (a widespread species also in Africa and Ceylon with at least 1 derivative in Madagascar)
Julianaceae (2/5) (but probably an artificial group)
Koeberliniaceae (1/1)
Krameriaceae (1/15)
Loasaceae (12/266 (plus 1 in Africa)) (several small genera in Mexico and SW U.S.)
Martyniaceae (3/13)

5) *Miscellaneous (aquatics or semiaquatics and Guayanan edaphic specialists)*

Cannaceae (1/55)
Cyrillaceae (3/13) (?) (in Europe in Eocene; mostly West Indian)
Mayacaceae (1/9 (also 1 in Africa))
Saccifoliaceae (1/1)
Sarraceniaceae (?) (3/17) (only 1 genus (6 spp.) in tropics)
Tepuianthaceae (1/5)
Thurniaceae (1/3)

* I have followed traditional familial limits. Rhabdodendraceae (2 species) was treated as a distinct family in Flora Neotropica. The other families listed by Prance (1978) as endemic are segregates (e.g., Peridiscaceae), erroneously listed (Pontederiaceae), or both (Heliconiaceae).

species each. Unlike most of their Palaeotropical counterparts, many of the Neotropical-restricted families are ecologically important. Bromeliaceae is one of the major epiphyte families; Cactaceae dominate many dry regions. Families like Caryocaraceae, Humiriaceae, and Vochysiaceae are important canopy trees of lowland tropical forests. To these may be added such speciose endemic groups as tribe Bignonieae of Bignoniaceae (Gentry, 1980a), which is the predominant group of Neotropical lianas; subfamily Lecythidoideae (Lecythidaceae; Prance & Mori, 1979), which is one of the predominant taxa of canopy trees of Amazonian forests; or subtribes Pleurothallidinae, Maxillarinae, and Oncidinae of the Orchidaceae, which together comprise nearly 5,000 species of Neotropical epiphytes (Dodson, pers. comm.).

It is noteworthy that many of the endemic families listed in Table 1 are taxa of dry, more or less subtropical habitats. The only endemic tropical North American families—Crossosomataceae, Fouquieriaceae, Garryaceae, Koeberliniaceae (disjunct to Paraguay), and Lennoaceae (also local in extreme northern Colombia)—are dry area specialists. Although endemic, basically South American families are more diversified ecologically, many of them, including Malesherbiaceae, Nolanaceae, and amphicontinental Cactaceae, Martyniaceae, Julianaceae, Krameriaceae, and Loasaceae are predominantly plants of dry areas.

Although these endemic taxa make an appreciable contribution to Neotropical species richness, the question of *why* families that evolved in the Neotropics have speciated more profusely than their Palaeotropical equivalents has not yet been addressed.

LAURASIAN TAXA

The phytogeographical significance of the new developments in plate tectonics was first brought into focus by Raven and Axelrod (1974). One of the major thrusts of the Raven-Axelrod synthesis was the fundamental difference between the floras of the northern or Laurasian continents and those of the now widely separated southern continents that were clustered together at the time of origin of the angiosperms. Even before plate tectonics became generally accepted, it had been realized that the high altitude South American flora was largely derived from north temperate sources and that the Panamanian isthmus had been a critical barrier to the southward migration of many northern taxa. One of the contributions of the Raven and Axelrod synthesis was pointing out the remarkable degree to which many plant families, even those shared by both North and South America, can be unambiguously referred either to the Gondwanaland or to the Laurasian floras on account of their general distributional patterns and the fossil record. They listed 51 basically Gondwanaland plant families (or equivalent units) that probably spread from South America to North America in the middle to late Cenozoic as the Isthmian barrier decreased, and an additional 54 families (or equivalents) whose original presence in North America was probably older but whose major presence there probably resulted from mid- to late-Cenozoic migration from South America. Similarly a list of 29 Laurasian families (or equivalents) whose major arrival in South America probably coincided with building of the Isthmus of Panama in late Miocene to Pliocene was suggested, nine of them qualified as perhaps already having had a prior presence in South America; 11

TABLE 2. Laurasian elements of the Neotropical flora. Numbers indicate Neotropical genera with known species numbers/species in those genera (+ Neotropical genera for which species estimates are unavailable/total species in those genera).

†Aceraceae	1/5		(Krameriaceae)	1/15	
Actinidiaceae	1/80		Labiatae (?)	14/489	(+13/1,594)
*Aquifoliaceae	1/150		†Lennoaceae	4/8	
Aristolochiaceae	3/182		Liliaceae	23/167	(+15/1,217)
†Balsaminaceae	1/2		*Lythraceae (?)	16/361	
*Basellaceae	3/7		Magnoliaceae		(+2/130)
Bataceae	1/1		Myricaceae		(+1/35)
Berberidaceae	1/24	(+1/450)	†(Nyssaceae)	1/1	
Betulaceae	3/5		Oleaceae	8/52	
Boraginaceae (?)	11/96	(+14/1,020)	Orobanchaceae	1/2	(+1/140)
Buxaceae	3/42		Papaveraceae	1/1	(+3/120)
Callitrichaceae (?)		(+1/25)	†Pinaceae	4/40	
Caprifoliaceae	1/2	(+4/458)	Plantaginaceae	1/1	(+1/265)
Caryophyllaceae	6/77	(+15/1,389)	†Platanaceae	1/7	
*Celastraceae	16/102	(+4/361)	Plumbaginaceae	2/7	
*Chloranthaceae	1/40		Polemoniaceae	4/33	(+5/276)
Cistaceae		(+3/120)	Primulaceae	2/4	(+2/210)
			Pyrolaceae	1/1	(+3/33)
Clethraceae	1/38		Rafflesiaceae	4/29	
Cornaceae	2/8	(+1/6)	Ranunculaceae	3/14	(+7/1,097)
Crassulaceae	3/25	(+4/515)	*Rhamnaceae	23/168	
†Crossosomataceae	1/4		Rosaceae	16/95	(+15/2,279)
Cruciferae	19/93	(+16/1,304)	*Sabiaceae (?)	2/47	
Cyrillaceae	2/13		Salicaceae	2/30	
Droseraceae	1/20		Saxifragaceae	12/85	(+5/730)
Empetraceae	1/1		Scrophulariaceae	70/853	(+4/185)
Ephedraceae (?)		(+1/40)	Staphyleaceae	2/5	(+1/30)
Fagaceae	4/164		Styraceae	1/3	(+1/130)
†Fouqueriaceae	2/8		Symplocaceae	1/160	
†(Garryaceae)	1/18		*Theaceae	7/84	(+2/130)
Gentianaceae	19/494		Theophrastaceae	3/107	
Geraniaceae	4/42	(+2/490)	Typhaceae		(+1/10)
†Hamamelidaceae	3/5		*Ulmaceae	6/17	(+2/110)
Hippocastanaceae	2/3		Umbelliferae	48/480	
Hydrophyllaceae	2/46	(+3/230)	Valerianaceae	5/44	(+1/200)
†Illiciaceae	1/1		*Vitaceae	2/3	(+3/505)
Juglandaceae	4/18				
			Total	416/5,229	(+157/15,834)

† = does not reach South America.
* = listed as moving from South America to North America by Raven and Axelrod (1974).

other predominantly Laurasian families were suggested as probable earlier arrivals in South America. As thus interpreted, the modern flora of tropical America is of remarkably bipolar composition, with the great majority of its plant families having clearly Laurasian or clearly Gondwanan affinities. From this perspective, one might anticipate that the Neogene mixture of two different floristic elements via the Central American isthmus could have had a major effect on increasing floristic diversity, perhaps almost doubling the resultant flora of each of the two major neotropical regions. Although such floristic interchange also occurred in the Palaeotropics, it was less direct, interrupted by large expanses of desert in North Africa and a persistent water barrier between the Sunda and Sahul shelves in Australasia.

However, my analysis (Tables 2–6) suggests that adding together of Laurasian

TABLE 3. Summary of transect data for plants over 1″ dbh in a 1,000 m² sample of lowland wet forest at Los Tuxtlas, Veracruz (precipitation of 4,100 mm a year) (Gentry, in prep.).

	No. Spp.	No. Ind.
Gondwanan Families		
Acanthaceae	1	1
Anacardiaceae	1	2
Annonaceae	2	5
Apocynaceae	3	5
Araceae	3	3
Araliaceae	1	2
Bignoniaceae	4	9
Bombacaceae	1	1
Capparidaceae	1	2
Caricaceae	1	2
Compositae	2	3
Convolvulaceae	1	1
Dilleniaceae	2	7
Euphorbiaceae	4	10
Flacourtiaceae	2	2
Hippocrateaceae	2	8
Lauraceae	5	9
Leguminosae	7	12
Malpighiaceae	4	7
Meliaceae	5	6
Menispermaceae	1	1
Monimiaceae	1	3
Moraceae	7	24
Musaceae	1	7
Myrtaceae	3	3
Palmae	4	113
Piperaceae	4	6
Polygonaceae	2	2
Rubiaceae	4	12
Sapindaceae	4	5
Sapotaceae	3	8
Solanaceae	3	5
Tiliaceae	2	3
Urticaceae[a]	3	22
Violaceae	3	10
Total	97	321
Laurasian Families		
Celastraceae	2	3
Rhamniaceae	1	2
Staphyleaceae	1	2
Ulmaceae	1	1
Total	5	8
Unassigned Families		
Malvaceae[b]	1	1
Verbenaceae	2	2
indet. (cf. *Fraxinus*)	1	1
Total	4	4

Total: 106 species, including 29 liana species. For a similar 1,000 m² sample in a South American or southern Central American forest with 4,100 mm of rain 170 species over 2.5 cm diam. would be expected (based on the regression of species numbers versus precipitation calculated from the 19 sites of Gentry, 1981, 1982, and in prep.). The Veracruz diversity is significantly lower than the expected inner tropical value (R. Perozzi, pers. comm.). Note the overwhelming preponderance of Gondwana-derived families.

[a] Assignment as "Gondwanan" tentative.

[b] The Los Tuxtlas genus is *Robinsonella*, an exclusively Central American (= tropical Laurasian?) genus, and the family may be fundamentally Laurasian in origin.

and Gondwanan elements has not greatly increased overall Neotropical floristic diversity. There are over 10 times as many Gondwanan-derived as Laurasian-derived Neotropical species. The northward migrating Gondwanan taxa have so overwhelmed the corresponding southward migrating Laurasian taxa numerically that the latter's contributions to the total Neotropical flora have generally been relatively insignificant. This pattern is especially prevalent in the tropical lowlands of Central America, which must once have been populated by a tropical Laurasian floristic equivalent of the endemic Central American herpetofauna (Savage, 1966), mammalian fauna (Patterson & Pascual, 1972) or avifauna (e.g., Cracraft, 1973) (see Raven & Axelrod, 1974: 625–626). Graham (1976, 1982) has shown that a few South American taxa such as *Dichapetalum*, *Casearia*, *Laetia*, *Symphonia*, *Gustavia*, and *Byttneria* had already reached Veracruz, Mexico by Miocene times. Yet the Paraje Solo palynoflora was dominated by temperate North American

TABLE 4. Amazonian-centered Gondwanan families. Numbers indicate Neotropical genera with known species numbers/neotropical species in those genera (+ Neotropical genera for which species estimates are unavailable/total species in those genera).

Anacardiaceae (?)	15/133	(+2/257)	(Lacistemaceae)	2/14	
Annonaceae	28/555	(+3/250)	Lauraceae	11/700	(+4/870)
Apocynaceae	64/687	(+2/125)	Lecythidaceae	11/275	
Bignoniaceae	72/631		Leguminosae	216/2,980	(+48/8,189)
Bixaceae	1/5		Loganiaceae	12/136	(+2/106)
Bombacaceae	20/187		Malpighiaceae	44/801	
Burseraceae (?)	5/102	(+2/120)	Meliaceae	8/125	
Caryocaraceae	2/24		Menispermaceae	17/142	(+1/30)
Chrysobalanaceae	8/334		Moraceae	23/408	
Cochlospermaceae	2/8		Myristicaceae	5/81	
Combretaceae	7/97		Ochnaceae	9/67	(+1/300)
Connaraceae	4/57	(+1/100)	Olacaceae	13/87	
Convolvulaceae	21/1,000		Palmae	52/1,110	(+3/42)
(Dialypetalanthaceae)	1/1		Polygalaceae	6/183	(+3/630)
Dichapetalaceae	3/43		Quiinaceae	4/53	
Dilleniaceae	5/60		Rhizophoraceae	5/24	
(Duckeodendraceae)	1/1		Sapindaceae	27/438	(+5/490)
Ebenaceae	2/82		Sapotaceae	9/208	(+3/234)
Elaeocarpaceae	4/7	(+2/125)	Simaroubaceae	11/106	
Euphorbiaceae	92/2,607		Sterculiaceae (?)	14/293	(+2/360)
Flacourtiaceae	28/267		Tiliaceae	20/139	
Gnetaceae	1/6		Trigoniaceae	1/24	
Hernandiaceae	3/22		Turneraceae (?)	1/60	(+2/26)
Hippocrateaceae	12/114		Violaceae	11/98	(+2/650)
Humiriaceae	8/46		Vochysiaceae	7/182	
Icacinaceae	13/56		Total	961/15,866	(+88/12,904)

elements. Similarly an Oligocene site in Puerto Rico (Graham & Jarzen, 1969) was characterized by the presence, although at reduced levels, of several of the same north temperate genera that today are disjunct in the midaltitude "bosque caducifolia" of Mexico: *Liquidambar, Fagus, Nyssa* as well as such other Laurasian taxa as *Myrica, Engelhardtia,* and *Hauya*. These taxa led Graham and Jarzen to emphasize prior, more direct migration between Mexico and the Greater Antilles. Nevertheless a number of tropical South American taxa that must have arrived over water were present.

As the Isthmian connection closed, additional South American taxa moved north to completely dominate the Central American lowlands. Most of this invasion has been so recent that even at the specific level there has been little differentiation. Thus, in groups like tribes Tecomeae and Bignonieae of Bignoniaceae, virtually all of the species that reach northern Central America are indistinguishable from South American taxa (compare Gentry, 1982c with Gentry, 1973). There are only one species of Tecomeae and seven of Bignonieae in Guatemala that are not also in Colombia and Venezuela. Perhaps this northward migration is still taking place. At any rate, there is a clear northward decrease in the number of species of many Neotropical families (Gentry, 1982a). It seems likely that, in general, individual tropical lowland forests in northern Central America may be less diverse than their southern equivalents, as suggested by Sarukhan (1968). Toledo (1982) has shown that within Mexico tree species rich-

TABLE 5. Andean-centered Gondwanaland groups. Numbers indicate neotropical genera with known species numbers/Neotropical species in those genera (+ Neotropical genera for which species estimates are unavailable/total species in those genera).

5a. Northern Andes

Acanthaceae	61/1,493		Loranthaceae	16/592	(+1/15)
Araceae	38/1,386		Marantaceae	10/270	(+1/11)
Araliaceae	5/197	(3/356)	Marcgraviaceae	4/125	
Balanophoraceae	7/15		Melastomataceae	85/3,153	
Begoniaceae	1/600		Monimiaceae	8/246	
Bromeliaceae	46/2,108		Musaceae	2/82	
Brunelliaceae	1/51		Myrsinaceae	12/311	(+2/600)
Campanulaceae	9/568	(+7/712)	Nyctaginaceae ?	27/277	(+3/160)
Cannaceae	1/55		Orchidaceae	306/8,266	
Caricaceae	3/29		Oxalidaceae	1/8	(+2/870)
Columelliaceae	1/4		Passifloraceae	4/362	
Compositae	502/3,864	(+87/7,202)	Piperaceae	4/25	(+2/3,000)
Cyclanthaceae	11/178		Rubiaceae	147/2,906	(+21/2,545)
*Ericaceae	37/731		Tovariaceae	1/2	
Gesneriaceae	40/917		Tropaeolaceae	2/92	
Guttiferae	21/232	(+3/590)	Urticaceae ?	7/88	(+6/653)
Haloragidaceae	1/1	(+3/58)	Zingiberaceae	4/111	
			Total	1,425/29,345	(+141/16,772)

5b. Southern Andes/South Temperate

†Aetoxicaceae	1/1		Loasaceae	12/266	
†Auraucariaceae	1/2		†Malesherbiaceae	1/27	
Calyceraceae	4/46		Myrtaceae	24/1,254	(+2/1,100)
Coriariaceae	1/1		†Myzodendraceae	1/11	
Cunoniaceae	3/12	(+1/170)	†Nolanaceae	1/18	
Cupressaceae	3/5		*Onagraceae	14/275	
†Epacridaceae	1/1		Podocarpaceae	1/37	
†Eucryphaceae	1/1		Portulacaceae	5/8	(+5/422)
†Frankeniaceae	3/8		Proteaceae	3/92	
†Gomortegaceae	1/1		†Restionaceae	1/1	
Hydnoraceae	1/6		Santalaceae	7/43	
Iridaceae	34/188	(+1/100)	Solanaceae	66/1,861	(+1/8)
Juncaceae	6/49		Winteraceae	1/1	
†Lardizabalaceae	2/3				
			Total	199/4,218	(+10/1,800)

† = does not reach Central America.
* = listed as moving from North America to South America by Raven and Axelrod (1974).

ness of the lowland tropical rain forest decreases dramatically northward. My data from a 1,000 m² sample of rich lowland rain forest in Veracruz also show fewer species than would be expected in a similar vegetation further south (Table 3). However, this pattern is shown only by lowland moist forest species: Mexican dry areas contrast in being very diverse, even in ultimately southern-derived taxa, with many endemic species (cf., Rzedowski, 1978: 75).

The relatively depauperate condition of lowland Central American forests may also have a much more recent origin and be due largely to Pleistocene climatic fluctuations. While drought has been considered the major effect of Pleistocene glaciation on the lowland tropics, Central America, at the margin of the tropics, may have been more affected by the concomitant general lowering of the temperature; many sensitive inner tropical taxa may have been eliminated or "con-

TABLE 6. Miscellaneous taxa. Numbers indicate neotropical genera with known species numbers/Neotropical species in those genera (+ Neotropical genera for which species estimates are unavailable/total species in those genera).

Guayana-centered groups		
Burmanniaceae	13/51	
Dipterocarpaceae	1/1	
Mayacaceae ?	1/9	
Podostemataceae	19/151	
Rapateaceae ?	15/79	
Saccifoliaceae	1/1	
Sarraceniaceae ?	1/6	
Tepuianthaceae	1/1	
Triuridaceae	4/12	
Total	56/311	
Dry-area Gondwanan groups		
Cactaceae	60/2,000	
Capparidaceae	10/40	(+4/416)
Erythroxylaceae	1/180	
Koeberliniaceae	1/1	
Martyniaceae	3/13	
Velloziaceae	4/229	
Zygophyllaceae	12/62	
Total	91/2,525	(+4/416)
Unassigned		
Aizoaceae	2/4	(+4/90)
Alismataceae	2/61	
Amaranthaceae	7/188	(+7/535)
Amaryllidaceae	26/799	(+3/210)
Asclepiadaceae	46/932	(+3/280)
Butomaceae	2/7	
Canellaceae	3/11	
Ceratophyllaceae	1/2	
Chenopodiaceae	10/34	(2/14)
Commelinaceae	17/163	
Cucurbitaceae	55/311	
Cyperaceae	8/88	(+18/3,738)
Dioscoreaceae	1/15	(+1/600)
Elatinaceae		(+2/45)
Eriocaulaceae	12/868	
Goodeniaceae	1/1	
Gramineae	127/838	(+80/4,692)
Haemodoraceae	1/2	
Hydrocharitaceae	8/20	
Juncaginaceae	2/5	
Lemnaceae	4/12	
Lentibulariaceae	3/116	
Linaceae ?	3/20	(+1/230)
Malvaceae	50/860	
Myoporaceae	1/1	
Najadaceae	1/8	
Nymphaeaceae	5/27	
Phytolaccaceae	13/78	(+2/38)
Polygonaceae	10/203	(+5/724)
Pontederiaceae	4/21	
Potamogetonaceae	5/42	
Rutaceae	36/233	(+4/313)
Taccaceae		(+1/30)
Thymelaeaceae	7/71	(+1/10)
Verbenaceae	40/1,143	
Xyridaceae	2/21	(+1/250)
Total	516/7,206	(+135/11,799)

fined southward'' by the slightly lower temperatures during glacial advances (Axelrod, pers. comm.). This may have been the ultimate fate of the tropical North American flora that is known to have inhabited even much of the southern and central United States during the Eocene and would be consistent with such patterns as the modern diversity of Sabiaceae, known to have been widespread in Tertiary North American tropical floras, which is greater in Panama and Costa Rica than it is in northern Central America (Gentry, 1981).

The northward movement of lowland tropical Gondwanan elements has had no significant counterpart of southward moving tropical Laurasian taxa. The most clearly Laurasian families to have noteworthy complements of species in lowland South American forests are Aristolochiaceae and Vitaceae, each with a single vine genus with numerous species in South America (*Aristolochia, Cissus*); not surprisingly, both are also well represented in the West Indies. Four other tropical lowland families of probable Laurasian derivation are characterized by affinity for dry areas and a strong representation both in the West Indies and in northern Central America. Three of these—Buxaceae, Boraginaceae, and Rhamnaceae—are proportionately better represented in temperate North America than in the Neotropics. In their dry area preference, these groups are reminiscent of the

endemic tropical Laurasian families previously noted. However, representatives of all of these families have penetrated into lowland South America. In the case of Buxaceae, penetration of South America is minimal (contrary to the distribution shown in Heywood, 1978) and restricted to a few limestone outcrops in northern Venezuela (*Styloceras* goes south in the Andes but may not be closely related; Gentry & Foster, 1981). Theophrastaceae has more recorded species in Peru than farther north but is a more predominant vegetational element and has greater generic diversity in Central America and the West Indies. One genus, *Clavija,* which links Theophrastaceae to Myrsinaceae, occurs in lowland tropical forests but is poorly represented in Amazonia and may have only a single species reaching coastal Brazil. Only two genera (*Cordia, Tournefortia*) of the twenty-four genera of Boraginaceae that reach the Neotropics penetrate the lowland tropical forests to any extent. Although Rhamnaceae were listed as basically Gondwanan by Raven and Axelrod (1974), the pattern shown by *Rhamnus* (Johnston & Johnston, 1978) seems typical of the group and points to a northern ancestry. As in Boraginaceae, the penetration of the family into lowland Neotropical forests is minimal (monotypic *Ampelozizyphus* and a few species of *Gouania* and *Colubrina*), although it is better represented in drier parts of South America.

While the lowland tropical South American flora would be almost imperceptibly changed if all of these putatively tropical Laurasian groups (a total of perhaps a few hundred species in all of lowland tropical South America) were eliminated, Laurasian taxa are much more important in Neotropical montane floras. In fact, there seems to be a basic dichotomy between the Laurasian-derived upland and Gondwanan-derived lowland neotropical floras. In Central American upland forests Laurasian elements clearly predominate ecologically with families like Pinaceae, Fagaceae, Juglandaceae, Magnoliaceae, Theaceae, and Ulmaceae especially important as canopy members of the temperate montane forests. These northern taxa gradually decrease southward so that families like Hamamelidaceae and Pinaceae do not cross the Río San Juan lowlands and are not present south of northern Nicaragua, while Garryaceae and many important genera of other families (e.g., *Ulmus, Celastrus,* most Juglandaceae) reach only upland Panama.

Even in South America, Laurasian elements tend to prevail in montane forests, ecologically, if not always in numbers of species. Many of these species are wind-pollinated and thus especially well represented in the fossil record. Consequently we may be reasonably confident that the palynological documentation of their recent arrival in South America is meaningful. Such knowledge of the history of Andean forests relies almost totally on the work of van der Hammen and his associates (summary in van der Hammen, 1974). The first montane elements to arrive at the Palynological sites in the Cordillera Oriental at the Sabana de Bogota were *Hedyosmum* and *Myrica,* as the Cordillera was uplifted during the Pliocene. By the beginning of the Pleistocene, the principal upheaval of the region was completed. During the earliest Pleistocene glacial advance the palynoflora of this region suggested a primitive and depauperate paramo vegetation including such ultimately northern-derived elements as *Aragoa* (Scrophulariaceae), *Hypericum* (Hypericaceae), Umbelliferae, *Plantago, Polylepis* (Rosaceae; perhaps southern), *Valeriana,* and Ranunculaceae. During the Pleistocene the palynoflora fluctuated

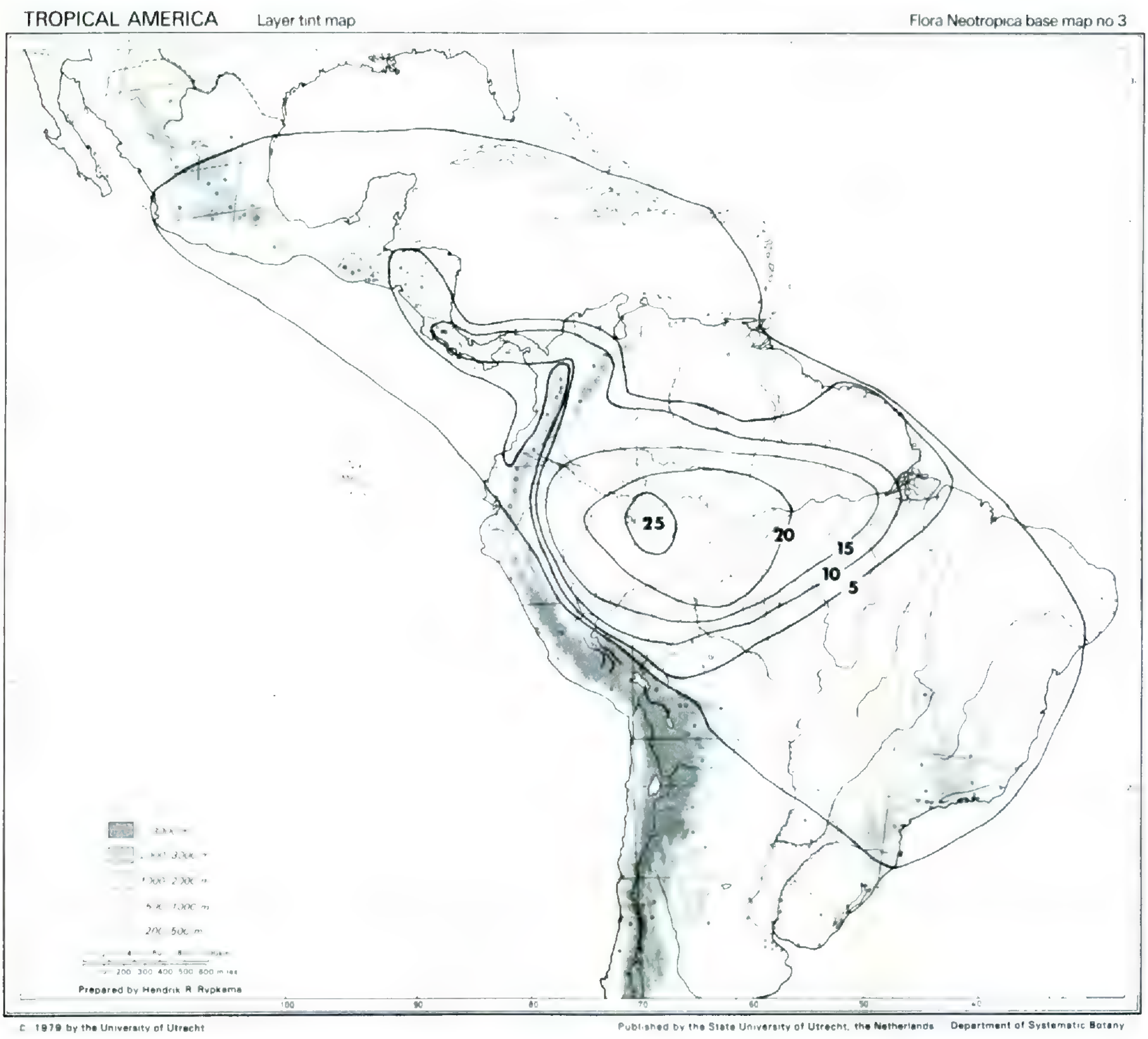

FIGURE 1. Typical Amazon-centered distribution of a taxon of canopy trees, Moraceae tribe Olmedieae. Tribal distribution with species diversity isohyets plotted from the data of Berg (1972: fig. 1). Note the concentration of species in (wetter) western Amazonia in the area of the Colombia/Brazil/Peru frontier. Additional collecting in poorly known northern Amazonian Peru and adjacent Colombia will probably extend the high diversity region westward.

with the changing altitudinal zonation of the vegetation brought about by climatic changes between glacial and interglacial periods. Both the paramo and montane forest floras were gradually enriched during the Pleistocene. In the lower Pleistocene, such additional northern elements as *Geranium*, *Gentiana*, *Lysipomia*, *Juglans*, and (perhaps southern) Urticaceae appear in the pollen record, along with southern taxa like *Gunnera* and phytogeographically problematical *Styloceras* (see Gentry & Foster, 1981). *Alnus* first arrived at the end of the lower Pleistocene and became dominant during the middle Pleistocene. *Quercus* first appeared approximately 250,000 years ago at the end of the Middle Pleistocene and thereafter increased progressively in importance. Although some southern taxa like *Weinmannia* also arrived in the Cordillera Oriental during the Pleistocene, northern elements prevailed and the present northern Andean forests are still dominated by Laurasian taxa.

Even today such northern families as Myricaceae, Juglandaceae, Betulaceae,

FIGURE 2. Extra-Amazonian or Andean-centered distribution of a taxon of "palmetto" (Zingiberaceae: subfamily Zingiberoideae; Maas, 1977: fig. 5; number of species per grid square).

Fagaceae, Magnoliaceae, Berberidaceae, Hippocastanaceae, Cyrillaceae, Clethraceae, Cornaceae, Oleaceae, and Caprifoliaceae are present in tropical South America almost entirely in the upland Andes. Within the Andes, there is a decrease in representation of these families farther south. For example, *Quercus*, the absolute dominant of most Colombian lower montane forests, does not occur in Ecuador. Other woody families like Salicaceae, Ulmaceae, Theaceae, Celastraceae, Aquifoliaceae, Sabiaceae, and Staphyleaceae, have one or two widespread species (or genera) that have become widespread in the tropical lowlands (respectively: *Salix humboldtiana*, *Trema micrantha* and *Celtis iguanea*, *Ternstroemia*, *Gouepia*, *Ilex inundata*, *Ophiocaryon*, *Turpinia occidentalis*). Interestingly, the lowland representatives of such taxa are often restricted in Amazonia to ecologically impoverished extreme sites such as seasonally inundated streamsides (*Salix*, *Ilex*, *Ophiocaryon duckei*, *Ampelozizyphus* (Rhamnaceae)), white sand substrates (many *Ternstroemia* and *Ophiocaryon*), or second growth (*Trema*, *Celtis*). Similarly, the only Amazonian species of south temperate *Podocarpus* is restricted to white sand (*Gentry et al. 28871* (MO) from near Iquitos, apparently an undescribed species).

Predominantly herbaceous Laurasian families have a greater tendency to be

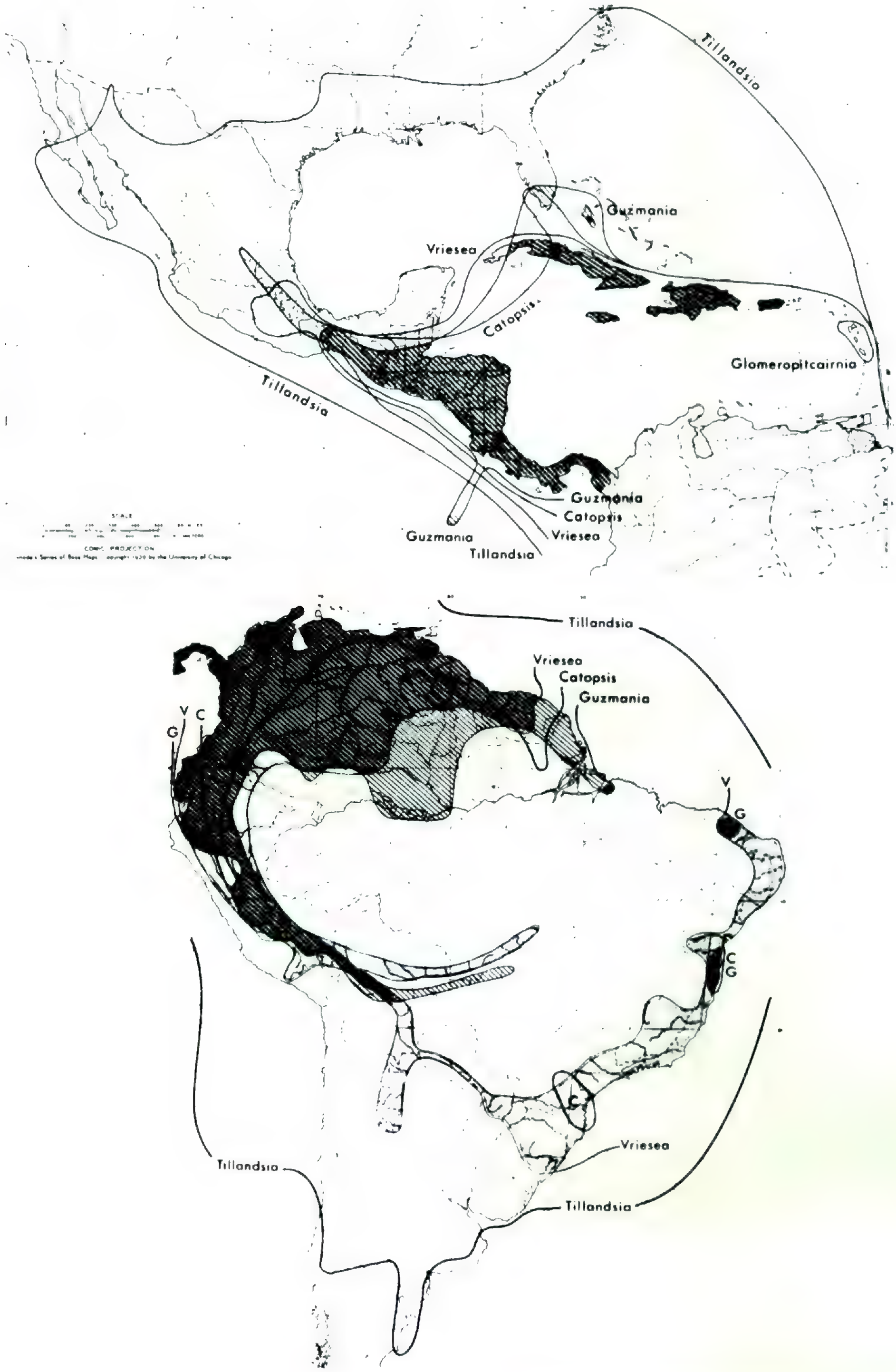

FIGURE 3. Extra-Amazonian or Andean-centered distribution of a predominantly epiphytic taxon (Bromeliaceae, subfamily Tillandsioideae; Smith & Downs, 1977: fig. 213).

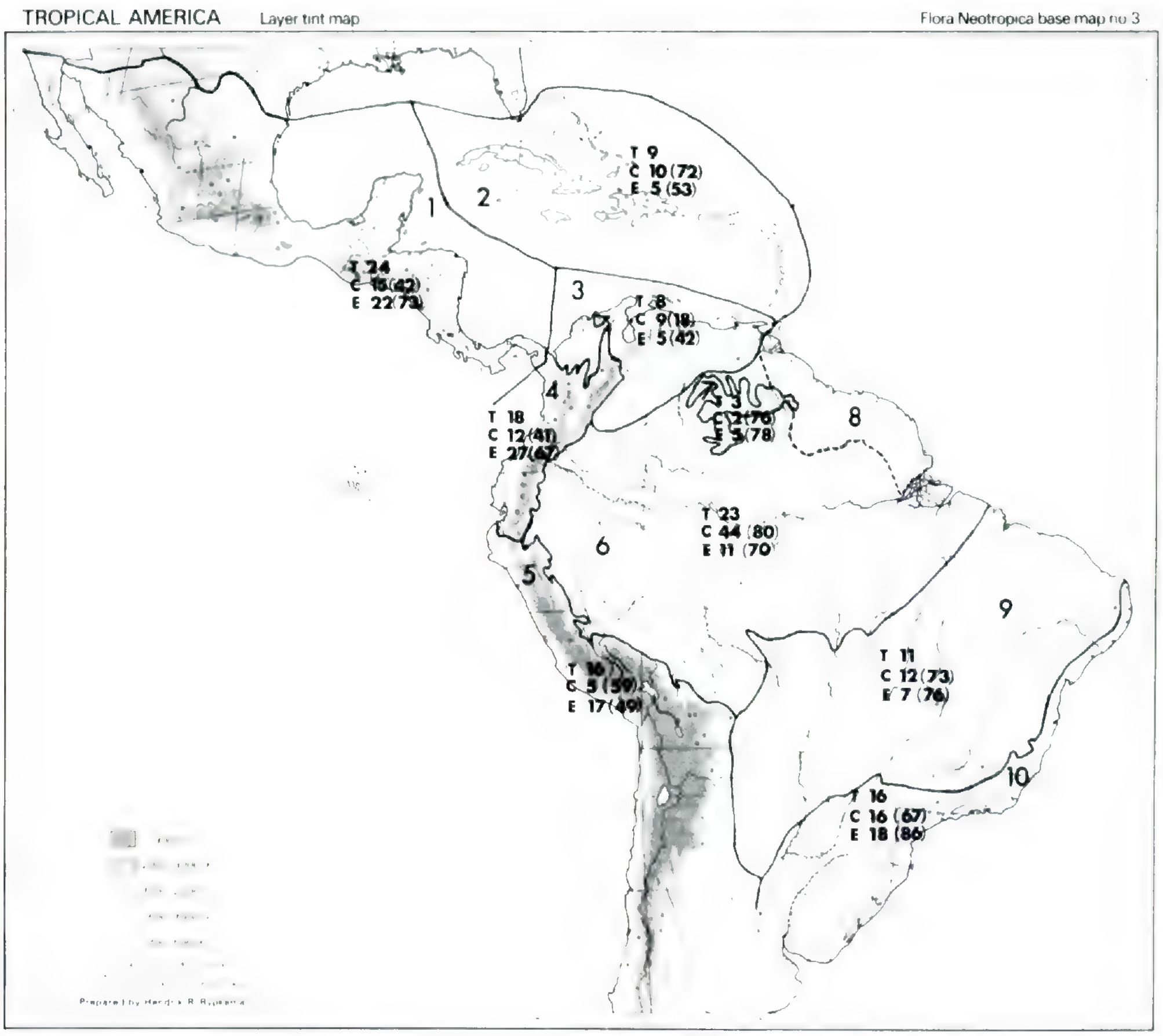

FIGURE 4. Neotropical phytogeographic regions. 1. Mexico and Central America. 2. West Indies. 3. Northern Venezuela-Colombia. 4. Northern Andes. 5. Southern Andes. 6. Amazonia (western border defined by 500 m contour). 7. Guayana Highlands (over 500 m). 8. Guiana subregion (included as part of Amazonia except for species not found elsewhere in Amazonia). 9. Cerrado and associated dry areas. 10. Coastal Brazil. Small numbers indicate percent of monographed species occurring in or endemic to each region. T = Percent of total sample of 8,117 recently monographed species occurring in that region. C = Canopy trees and lianas: percent of the species of taxa characterized by habit occurring in each region (percent of region's species of that habit group which are endemic to the region in parentheses). E = Epiphytes and palmettos: percent of the species of taxa characterized by habit occurring in each region (percent of region's species of that habit group which are endemic to the region in parentheses). See Tables 7, 8, 9 for complete data.

weedy and their patterns are not so well marked. Nevertheless, except for a few weeds, families like Crassulaceae, Caryophyllaceae, Ranunculaceae, Cruciferae, Saxifragaceae, Rosaceae (s.s.), Plumbaginaceae, Geraniaceae, Callitrichaceae, Balsaminaceae, Umbelliferae, Primulaceae, Gentianaceae, Polemoniaceae, Hydrophyllaceae, Scrophulariaceae, Orobanchaceae, and Plantaginaceae are much better represented in the montane Neotropics than in the lowlands.

For both trees and herbs there is a strong dichotomy between the noticeable presence of Laurasian taxa in montane forests and their virtual absence in the lowlands.

Most of the Laurasian taxa, especially the woody ones, have speciated rather little in the Andes (see Gentry, 1982a). Presumably this reflects in part their recent arrival. As a result, the impressive list of 72 Laurasian-derived Neotropical families in Table 2 accounts for a very small percentage (<10%) of the total Neotropical flora and virtually none of that of the lowland tropics.

Gondwanan Taxa

The major components of the Neotropical flora are Gondwanaland-derived groups (Tables 4–6). However, there is a fundamental phytogeographic difference within this group, for these autochthonous South American families fall consistently into two major distributional groups. Many of these families are centered in Amazonia (Table 4; Fig. 1) and may be referred to as Amazonian-centered. Most of the remainder are fundamentally and contrastingly extra-Amazonian with very poor representation in Amazonia and usually have their distributional centers in the Andes, especially the northern Andes (Table 5; Figs. 2, 3). These taxa may conveniently be termed Andean-centered taxa although their main diversity is reached in the lowlands near the base of the mountains and in middle elevation cloud forests rather than in the high mountains themselves.

I first became aware of these two striking patterns in the field. In order to document them, I extracted and compiled distributional data for recently monographed Neotropical families and large genera, beginning with the Flora Neotropica monographs, but also including as many other Flora Neotropica-caliber revisions of major taxa as I could find in major systematic botany journals for the last ten to twenty years. This yielded a data set of 8,117 monographed species. Subdividing the Neotropics into the nine phytogeographic regions shown in Figure 4, and counting the number of monographed species occurring in each region provided the data summarized in Tables 7 and 8. The great majority (71% or almost 5,800 species) of monographed species belong to families that are either clearly Amazonian-centered (3,052 spp.) or clearly northern-Andean-centered (2,715 spp.). The component families of each of these major phytogeographical groups not only show strikingly concordant distributional patterns but also amazing consistency ecologically. The Amazonian-centered taxa are overwhelmingly canopy trees and lianas; the extra-Amazonian ones are chiefly shrubs, epiphytes, and palmettos.

Amazonian-centered Taxa

The Amazonian-centered taxa include 38% of the total data set of monographed species. These families have an average of almost half (44%) of their species in Amazonia. Virtually all of these taxa are predominantly canopy trees and lianas; moreover, almost all canopy trees and lianas of the Neotropical lowlands belong to these Amazonian-centered groups. These taxa are conspicuously under-represented in the Andes; on the average only 12% of their species occur in the northern Andean region and only 5% in the Southern Andes. They are well represented in the coastal Brazil region (16% of their species), which constitutes a distinct secondary center for most of them; however, not a single one of these monographed major taxa has as many species in coastal Brazil as in Amazonia,

TABLE 7. Number of species and endemism in monographed taxa by predominant habit group and geographical distribution. Number of endemic species for each region in parentheses.

Habit[1]	Amazonia	Coastal Brazil	Cerrado & Caatinga	North. Andes	South. Andes	Central America & Mexico	North. Venezuela & Colombia	West Indies	Guayana Highland	Lowland Guiana[2]
Canopy trees and lianas	1,334 (1,072)	482 (322)	373 (272)	373 (154)	144 (85)	453 (189)	280 (56)	312 (226)	55 (42)	177 (57)
Epiphytes and palmettos	292 (205)	498 (426)	184 (140)	723 (481)	469 (231)	607 (443)	142 (59)	130 (69)	140 (109)	57 (38)
Herbs and shrubs	60 (16)	140 (76)	167 (103)	128 (51)	437 (231)	559 (319)	107 (9)	151 (41)	—	4 (2)
Vines[3]	75 (40)	74 (40)	45 (18)	126 (73)	78 (40)	132 (65)	47 (11)	55 (30)	1 (1)	9 (9)
Montane trees[4]	7 (5)	12 (8)	3 (1)	71 (47)	57 (39)	98 (84)	22 (7)	27 (20)	8 (6)	—
Arid area trees	—	2 (1)	17 (12)	4 (1)	47 (37)	37 (30)	8 (3)	9 (4)	—	—
Miscellaneous[5]	61 (52)	80 (67)	143 (130)	29 (12)	31 (20)	48 (35)	22 (8)	38 (34)	13 (10)	47 (43)
Total (8,117)	1,829 (1,390)	1,288 (940)	932 (676)	1,454 (819)	1,263 (683)	1,934 (1,165)	628 (153)	722 (424)	217 (168)	294 (149)
Percent of species occurring in region	23%	16%	11%	18%	16%	24%	8%	9%	3%	4%
% Endemism[6] (total = 6,567/8,117 = 81%)	76%	73%	73%	56%	54%	60%	24%	59%	77%	—
Total endemism[7]	17%	12%	8%	10%	8%	14%	2%	5%	2%	2%

[1] Predominant habit of monographed taxon.
[2] Figures for Guianas subregion include only those species that occur in the lowland Guianas but not also in Amazonia.
[3] Distribution primarily reflects pattern of single large family—Passifloraceae (363 spp.).
[4] Betulaceae, Brunelliaceae, Clethraceae, Juglandaceae, *Polylepis*, Podocarpaceae, *Rhamnus*, *Colubrina*, Sabiaceae. Rhamnaceous taxa include many Mexican desert shrubs.
[5] Parasites, aquatics, Velloziaceae, Proteaceae.
[6] Endemic species in region as percent of total monographed species in that region.
[7] Endemic species in region as percent of total species in all monographed taxa.

TABLE 8. Percent distribution of monographed taxa by predominant habit group and geographical distribution.

Habit[1]	Total Spp.	Amaz.	Coast. Braz.	Cerrado & Caatinga	North. Andes	South. Andes	Central Amer. & Mexico	N. Venezuela & Colombia	West Indies	Guayana Highland	(Guianas)[2]
		Percent of Species[3]									
Canopy trees and lianas	3,052	44	16	12	12	5	15	9	10	2	(6)
Epiphytes and palmettos	2,715	11	18	7	27	17	22	5	5	5	(2)
Herbs and shrubs	1,034	6	14	16	12	42	54	10	15	—	—
Vines[4]	459	16	16	10	27	17	29	10	12	—	(2)
Montane trees[5]	256	3	5	1	28	27	38	9	11	3	—
Arid area trees	105	—	2	16	4	45	35	8	9	—	—
Others (parasities, aquatics, Velloz., Proteac.)	496	12	16	29	6	6	10	4	8	3	(9)
Total	8,117										

[1] Predominant habit of monographed taxon.

[2] Figures for Guianas subregion include only those species that occur in the lowland Guianas but not also in Amazonia.

[3] Percents total to more than 100% since widespread species are counted in each region in which they occur.

[4] Distribution primarily reflects patterns of single large family—Passifloraceae (363 spp.).

[5] Betulaceae, Brunelliaceae, Clethraceae, Juglandaceae, *Polylepis*, Podocarpaceae, *Rhamnus*, *Colubrina*, Sabiaceae. Rhamnaceous taxa include many Mexican desert shrubs.

not even Dilleniaceae, whose strong representation in the coastal region was emphasized by Kubitzki (1975). Many of the Amazonian-centered families have derivative species in the cerrado and associated dry areas of the Brazilian shield (12% of the species); in almost every case the cerrado species are shrubs or subshrubs in taxa that are otherwise trees or lianas. These groups are markedly poor in the West Indies (10% of the species on the average, with a disproportionate part of that total due to the evolutionary explosion of a single otherwise small section of *Tabebuia*).

The Amazonian-centered taxa are poorly represented in Central America (only 15% of their species), which is rather surprising since they make up nearly all of the moist and wet forest canopy of the Central American lowlands, just as in Amazonia. Most of the species of these taxa that do reach Central America are not endemic; rather, they are mostly those few Amazonian species that happen to have unusually wide ranges. Thus, only 6% of the 3,000 monographed species of Amazonian-centered taxa are endemic to Central America. This contrasts with 80% endemism in Amazonia, where 35% of all the species of these taxa are endemic. Within Central America there is a marked decrease in the representation of Amazonian-centered taxa from south to north. Most of these families have several species reaching eastern Panama, noticeably fewer reaching western Panama and Costa Rica, and none crossing the Holdridge system tropical/subtropical delimitation at 12°N latitude in Nicaragua (exactly the same latitude as the diversity-reducing Isthmus of Kra in Malaysia!). Those Amazonian-centered families that do extend farther into Central America typically have only one or two species north of Nicaragua (see Gentry, 1982a, for specific examples of these patterns). Nevertheless, the relatively few Amazonian-centered taxa that reach northern Central America continue to constitute virtually all of the lowland forest canopy (Table 3 and Gentry, in prep.).

An interesting subsidiary pattern is shown in Central America by several of these taxa. Several of the groups have a distinct secondary radiation in northern Central America. A good example is provided by Bignoniaceae with tribe Crescentieae having three genera and 35 species almost exclusively in Central America (Gentry, 1979, 1980a). Although derived from the fundamentally South American tribe Tecomeae, Crescentieae are so distinct from that group in such important features as indehiscent fruits and bat-pollinated flowers that they have sometimes been treated as a distinct family (see Gentry, 1974a). Clearly Crescentieae reflect a long history of differentiation in Central America subsequent to an initial colonization by South American Tecomeae stock. Yet most other Central American Bignoniaceae are undifferentiated from their South American progenitors even at the species level.

It is tempting to think of such patterns as reflecting a two pulse migration: (1) early colonization by island hopping across the proto-Antilles at the end of the Cretaceous with subsequent major differentiation and (2) a major migration subsequent to closing of the Isthmus of Panama that was too recent to permit much generic, or even specific, differentiation.

ANDEAN-CENTERED TAXA

The second major Neotropical phytogeographic pattern, contrastingly extra-Amazonian, may be referred to conveniently as Andean-centered and is almost

the mirror image of that shown by the Amazonian-centered taxa. In those regions where Amazonian-centered taxa are well represented, Andean-centered taxa are poorly represented and vice versa. Families with this pattern have their distributional centers in the northern Andes, where over a fourth (27%) of their species occur, and are also well represented in the southern Andes (17% of their species) (Table 8). These groups are predominantly epiphytic (Araceae, Araliaceae, Bromeliaceae, Cyclanthaceae, Ericaceae, Gesneriaceae, Guttiferae, Piperaceae/*Peperomia*, Orchidaceae, etc.), understory shrubs (Acanthaceae, Caricaceae, Melastomataceae, Monimiaceae, Myrsinaceae, Piperaceae, Rubiaceae, Solanaceae), and coarse palmetto-type monocots (Musaceae, Marantaceae, Zingiberaceae). These groups are not only conspicuously under-represented in Amazonia (11% of their species), they are also poorly represented in the dry cerrado-caatinga region (7% of their species). Like the Amazonian-centered group, they are well represented in the coastal Brazil region (18% of their species) and poorly represented in northern Venezuela and the West Indies.

Unlike their Amazonian-centered counterparts, the Andean-centered taxa are very well represented in Central America, especially Costa Rica and Panama, where 22% of their species occur. Southern Central America is clearly a major secondary center of speciation for most of these groups. Although some of these groups actually appear to have more species in Costa Rica or Panama than in the northern Andes, this may be mostly an artifact of the much poorer floristic data base from northwest South America. In any event, these groups account for most of the incredible floristic diversity of the Choco region (Gentry, 1982a). The Andean-centered taxa show very pronounced endemism in Central America, with 73% of the Central American species endemic. This is in strong contrast to the low (42%) Central American endemism of Amazonian-centered taxa (Table 9). Clearly both Central America and western South America have been major evolutionary centers for these groups.

Although representation of these taxa is highest in mountainous phytogeographic regions, it should be re-emphasized that high species diversities do not occur at high altitudes but rather in the wet lowland and premontane cloud forests along the base and lower slopes of the mountains.

These two dominant phytogeographic patterns—Amazonian-centered trees and lianas and Andean-centered palmettos, shrubs, and epiphytes—together account for the great majority (71% of my sample) of Neotropical plant species. Together these families, all basically Gondwanan, absolutely dominate the lowland neotropical flora, both in Central and South America. Thus any explanation of the patterns of evolutionary diversification in these taxa will largely explain the richness of the Neotropical flora.

Dry-area-centered Taxa

A few subsidiary distributional patterns need to be mentioned. One is that of taxa with distributional centers in dry areas and poor representation both in Amazonia and the moist Andes. Three good examples are Capparidaceae, Cactaceae, and Zygophyllaceae. Amaranthaceae and possibly Chenopodiaceae, the latter often specialized for the highly alkaline conditions typical of deserts, are also better represented in dry than in wet areas. Dry-area-centered taxa tend to be largely shrubs and herbs although some well known tree genera like *Prosopis*

TABLE 9. Relative endemism of phytogeographic regions. Percent of those species occurring in each region that are endemic.

Habit[1]	Total % Endemic to 1 Reg.	Amaz.	Coast. Brazil	Cerrado & Caatinga	North. Andes	South. Andes	Central Amer. & Mexico	N. Venezuela & Colombia	West Indies	Guayana Highland
Canopy trees and lianas	81	80	67	73	41	59	42	18	72	76
Epiphytes and palmettos	81	70	86	76	67	49	73	42	53	78
Herbs and shrubs	82	27	54	62	40	53	57	8	27	—
Vines[2]	71	53	54	40	58	51	49	23	55	100
Montane trees[3]	85	71	67	33	66	68	86	32	74	75
Arid area trees	84	—	50	71	25	79	81	38	44	—

[1] Predominant habit of monographed taxon.

[2] Distribution primarily reflects patterns of single large family—Passifloraceae (363 spp.).

[3] Betulaceae, Brunelliaceae, Clethraceae, Juglandaceae, *Polylepis*, Podocarpaceae, *Rhamnus*, *Colubrina*, Sabiaceae. Rhamnaceous taxa include many Mexican desert shrubs.

and *Bulnesia* also show this pattern. These groups are best represented in the southern Andean region (42% of their species), here including part of the monte, and the Central American region (54% of their species), especially Mexico and northern Central America. Not surprisingly, taxa adapted to dry areas are also relatively well represented in the northern Venezuelan-Colombian region and the dry cerrado-chaco-caatinga region of the Brazilian shield.

Although representation of these taxa is about as strong in the Southern Andean region as in the Central American region, endemism is slightly greater in Central America (57% vs. 53% of the region's species) and even more pronounced in the cerrado region (62%). Rzedowski (1962, 1978) has pointed out that endemism in Mexico is most striking among dry area taxa even though species of lowland tropical forests dominate the country's flora in terms of absolute numbers. Despite the high endemism, taxa ultimately derived from the south strongly predominate in the Mexican dry area flora, in contrast to the north temperate-derived dry area flora of the United States deserts (Rzedowski, 1973). Such patterns, especially the prevalence of a preponderance of well-marked endemic families like Fouqueriaceae, Lennoaceae, Crossosomataceae, Malesherbiaceae, and Cactaceae in dry areas, have been cited (e.g., Rzedowski, 1962, 1978) as evidence of a long evolutionary history of dry taxa, implying the uninterrupted persistence of dry areas at least through most of the Cenozoic. Axelrod (1979) suggests that much of the early evolution and differentiation of dry area taxa may have been in edaphically dry areas with taxa spreading as dry climates expanded in the late Tertiary and Quaternary times. Whether originally edaphically restricted or not, the strong differentiation of many of these groups in Mexico and northern Central America implies that some of their ancestors may well have arrived via late Cretaceous island hopping (cf. Bignoniaceae, tribe Crescentieae above, most of whose members are specialized for such edaphically dry substrates as limestone outcrops and seasonally inundated savannahs).

It should be noted that, although amphitropical range disjunctions of dry area taxa are frequent, many of these surely reflect recent long distance dispersal (Raven, 1963), rather than the ancient patterns emphasized above. Moreover, although many of these dry area taxa might seem to be autochthonously Mexican and northern Central American based on their preponderance of species there, most of them are either clearly of Gondwanan affinities or presumably so by phytogeographic analogy. Thus the high species numbers of dry area adapted shrub and herb taxa in Mexico and adjacent regions are probably mostly a secondary phenomenon resulting from active evolutionary diversification in response to the increasingly dry climatic regimes of the Pliocene and Pleistocene, rather than necessarily due to ancient arrival or autochthonous origin. Genera disjunct between Chile and California, for example, are all prime candidates for long distance dispersal (Carlquist, 1982). Even some amphitropical dry-area shrubs like *Larrea* are now generally believed to result from relatively recent long distance dispersal rather than ancient distributions (Wells & Hunziker, 1976). Clearly range disjunctions of dry area plants must be interpreted on an individual basis.

While these dry area taxa are a significant and interesting component of the Neotropical flora, they are relatively unimportant in terms of overall Neotropical species richness, just as Rzedowski (1962) noted for Mexico.

MISCELLANEOUS SUBSIDIARY PATTERNS

A few other Neotropical phytogeographical patterns merit special note. Coastal Brazil is noteworthy for the concentration of often primitive species in a restricted area (e.g., Kubitzki, 1975; Soderstrom & Calderon, 1974) and some of the archaic taxa of coastal Brazil—e.g., primitive Dilleniaceae (Kubitzki, 1975), Bambuseae (Soderstrom & Calderon, 1974), *Perianthomega* (intermediate between the two main tribes of Bignoniaceae and perhaps close to the ancestral stock of the neotropical Bignonieae), a *Cecropia* with the simply spicate female inflorescence of African *Musanga* (Berg, pers. comm.)—may date from the Cretaceous separation of South America and Africa. Nevertheless no family has its distributional center in coastal Brazil. The same families that are well represented there are invariably better represented either in Amazonia or the Andes. However, both the recently uplifted Andes and most of Amazonia, which was underwater into the Pleistocene, are relatively recent entities geologically speaking, and the apparent prevalence of unspecialized taxa in Coastal Brazil may suggest the importance of this region as a source area for other phytogeographic regions.

Another rather isolated lowland area noted for its endemism (Gentry, 1982a) is the Chocó region of Pacific coastal Colombia and adjacent Ecuador. This rich, perhumid, but geologically young, region is an important subset of what is here termed the Northern Andean region. The floristic significance of the Chocó area is almost entirely at the species level although it does have a few endemic genera like *Trianaeopiper* (Piperaceae) and *Cremosperma* (Gesneriaceae). No family has its chief center of distribution in Chocó other than as part of the Northern Andean region.

Finally the Guiana Region, and especially the Guayana Highlands, are well known as areas of high endemism and much phytogeographic interest (Maguire, 1970). Geologically this area is very old, and the plants of the tepui summits have had the potential for very long periods of evolution in isolation. Nevertheless, exchange between summit flora and the lowland forest flora that ascends the tepui slopes has apparently been much more extensive than once thought (compare Steyermark, 1979, and Maguire, 1970). Even many of the species of the summits are shared with the lowlands, which are in turn no more than a northern phytogeographic subset of Amazonia. To be sure, there are a few strikingly distinct endemic species and genera in the region that might be recognized as distinct families—Saccifoliaceae (close to Gentianaceae), and Tepuianthaceae (close to Rutaceae). More intriguing are several non-endemic families that are found in the Neotropics only in the Guayana region. These include Sarraceniaceae (disjunct from North America), Tetrameristaceae (two monotypic genera, the other in Asia), and Dipterocarpaceae (see Maguire & Ashton, 1978; the opposing view that *Pakaraimea* is closer to Tiliaceae (Kostermans, 1978) is based on weak evidence and is phytogeographically irrelevant since the South American taxon clearly belongs to the Dipterocarpaceae ancestral plexus, no matter where the taxonomic limits are drawn). Such patterns suggest ancient survivals, not active evolutionary diversification.

A very few small families do have their centers of Neotropical diversification in the Guayana area. The only generally accepted families that seem to show this

pattern are Burmanniaceae, Podostemaceae, Triuridaceae, Mayacaceae, Thurniaceae, and Rapateaceae. Together they account for a total of not more than some 300 species. All are specialized for unusual life styles, as saprophytes, aquatics, or semiaquatics. In general the overall floristic significance of the Guayana area, and especially the Guayana Highlands, now seems very much less than earlier believed. If the 3% of my data set of monographed species that occur in the Guayana Highlands is any indication, the total flora of that region is minuscule indeed, even when allowance is made for the relatively small area of upland Guayana. On the other hand, the famed high endemism of the Guayana highlands, although much less than the 90% suggested by Maguire (1970), is somewhat supported by my data set. The 77% endemic species of the Guayana Highlands is slightly higher than the similar figure for any other phytogeographic region (Table 7).

Two other regions that are surprisingly depauperate in plant species as judged from this data set are the West Indies and the northern Venezuela/Colombia region, with respectively 9% and 8% of the total of monographed species. The 59% endemism value for the West Indies is almost identical to the 60% overall specific endemism of Central America, but the 24% figure for northern Venezuela/Colombia is by far the lowest such figure for any of these phytogeographical regions. In this light it is clear how Steyermark (1979) was able to achieve such a fine scale in delimiting centers of endemism in Venezuela, some centers based on as few as two species. With such low total endemism, even a few endemic species become noteworthy.

Floristic Summary

To summarize Neotropical floristic patterns, we have two major dichotomies. The first is between the basically Laurasian montane flora and basically Gondwanan lowland flora. The second, within the predominant latter group, is between a large group of families with Amazonian distributional centers, and a second important group that has distributional centers in the Andes, especially the northern Andes, and tends to be poorly represented in Amazonia. It is now clear that the Laurasian/Gondwanan dichotomy results from the separation of North and South America through most of Cenozoic time. The fundamental dichotomy between Amazonian- and Northern Andean-centered families, although equally clear cut, has not previously been generally recognized.

Virtually all lianas and canopy trees of the lowland Neotropics belong to Amazonian-centered taxa. Canopy trees of montane forests come from both Laurasian and Gondwanan groups with a gradation in the relative importance of the two from north to south. Epiphytes, understory shrubs, and palmettos mostly belong to Gondwanan groups with northern Andean distributional centers. Many Neotropical herbs are from widespread predominantly north temperate groups; like Gondwana-derived herb taxa they have extra-Amazonian distributional patterns. Vines (as opposed to lianas) are represented in both Laurasian and Gondwanan groups; however, it is noteworthy that the only representatives of clearly Laurasian families to extensively invade the lowland Neotropics are vines (*Aristolochia, Cissus, Gouania*) mainly occurring in forest edge situations rather than

mature forest. Shrubs are best represented in dry areas and typically show an amphitropical pattern with distributional centers both in northern Central America and the southern Andean region.

EVOLUTIONARY IMPLICATIONS

These very distinctive phytogeographic patterns suggest radically different speciation patterns in different regions and among the different adaptive types. Especially noteworthy are the differences (1) between upland, largely Laurasian, taxa and lowland, predominantly Gondwanan, groups and (2) within the latter group between the predominant Amazonian-centered and Andean-centered groups.

One striking differential is in pollination ecology. Almost half of the families of Laurasian-derived trees are wind-pollinated whereas virtually none of the Gondwanan angiosperm families is. Many of the northern Andean-centered groups are largely, or even predominantly, hummingbird-pollinated (e.g., Acanthaceae, Bromeliaceae, Campanulaceae-Lobelioideae, Ericaceae, Gesneriaceae, Loranthaceae-Loranthoideae, Marcgraviaceae, Musaceae, Tropaeolaceae, Zingiberaceae) whereas this pollination system is rather uncommon in other groups (e.g., a few Gentianaceae, Labiatae, Lythraceae, Polemoniaceae, Scrophulariaceae among Laurasian taxa; some miscellaneous species of Apocynaceae, Bignoniaceae, Combretaceae, Convolvulaceae, and Leguminosae among Amazonian-centered taxa). Plants with rather conspicuous, often large, tubular flowers pollinated by specialized large and medium-sized bees mostly belong to Amazonian-centered families (Apocynaceae, Bignoniaceae (Gentry, 1974a, 1974b), Cochlospermaceae (Frankie & Baker, 1974), Lecythidaceae (Prance, 1976; Mori et al., 1978), many Leguminosae (Frankie & Baker, 1974; Frankie et al., 1982)), but are also found among other groups (e.g., Marantaceae, Orchidaceae, Passifloraceae, Zingiberaceae). Even some Laurasian groups that are mostly large-bee pollinated in the temperate zone tend to have Neotropical representatives with other pollination systems (e.g., Scrophulariaceae, most of whose Neotropical genera have tiny inconspicuous flowers). Taxa having mostly species with small generalist-pollinated flowers (sensu Frankie et al., 1974, 1983; Gentry, 1982b) are well represented in all phytogeographical groups and show no obvious trends.

A related difference between phytogeographical/habit groups lies in their probable modes of speciation. Woody Laurasian taxa, largely wind-pollinated, have speciated very little in South America, even in the Andes where they are ecologically dominant. Even in Central America these plants have produced relatively few species. Ecotypic differentiation is frequent in some groups, for example among oaks in Costa Rica where different sets of related species tend to be restricted to different Holdridge life zones (Burger, 1977, pers. comm.). The general pattern of little speciation in these taxa is consistent with expectations based on the long generation times of woody plants, coupled with the relatively recent arrival of most of the taxa in South America and even southern Central America. It is also consistent with models that emphasize the importance of plant-pollinator interactions in promoting speciation, a potential patently unavailable to wind-pollinated species.

The woody Amazonian-centered canopy trees and lianas are the groups that show biogeographic patterns consistent with classical zoological models of allo-

patric speciation. These are the taxa that have the kinds of distributions that have been interpreted as resulting from speciation and/or survival in Pleistocene forest refugia. For example, Prance (1973) selected entirely woody Amazonian-centered taxa (Caryocaraceae, Lecythidaceae, Chrysobalanaceae, and Dichapetalaceae) to demonstrate the kinds of correlated patterns of restricted distributions—allopatric among closely related species but replicated in unrelated groups—that fit the predictions of the Pleistocene refuge model of tropical forest speciation. It is not surprising that Forero (1976) and Lleras (1978), both working with taxa of woody lianas, noted similar patterns in their groups. In these taxa outcrossing is the rule (Bawa, 1974), chromosome numbers are frequently high ("palaeopolyploidy") and often stable in a genus or family (Goldblatt & Gentry, 1980; Ehrendorfer, 1970), and hybridization is rare or non-existent (Ehrendorfer, 1970; Ashton, 1969). Major shifts in mode of pollination may be rare while speciation leading to specialization in such marginal habitats as white sand "campinarana" forests or seasonally inundated "varzea" or "tahuampa" forests is a major evolutionary theme (Gentry, 1980b, 1982d, 1982e). In general, closely related species show allopatric distributions and speciation seems somehow orderly with relatively few species per genus (14 spp./genus on the average with only 19 genera having over 100 species) and community diversity perhaps approaching a regulated ecological equilibrium (Gentry, 1982b).

The epiphytes, understory shrubs, and palmettos that make up most of the northern Andean-centered taxa are characterized by what appears to have been explosive speciation and adaptive radiation, almost certainly much of it sympatric. Genera are typically large (20 species per genus on the average; at least 120 genera with over 100 species). While it is conceivable that microgeographic speciation could explain much of the high diversity of typical Andean-centered taxa, my (Gentry, 1982a) attempt to fit the Chocó flora to the expectations of the Pleistocene refuge model were distinctly equivocal with very many local endemics occurring scattered throughout the region and constituting veritable "species swarms" in large evolutionarily plastic genera like *Anthurium, Piper,* and *Cavendishia*. The same patterns are documented by monographs of specific Andean-centered taxa (e.g., Harling, 1958; Smith & Downs, 1974, 1977, 1979; Berry, 1980; Luteyn, 1983). Berry (1980 and in prep.) suggested from his analysis of speciation patterns in *Fuchsia* that speciation in this group might reflect "shifting balance" phenomena (Wright, 1977; Templeton, 1980) with major genetic reorganizations or genetic transilience (Templeton, 1980) optimized both by the small localized populations and the need for constant recolonization of a habitat partitioned by mountains, local rainshadows and other climatic effects, vertically shifting cyclically coalescing and separating vegetational zones, and frequent landslides, which regularly provide open areas for colonization. The relatively short generation times of these herbaceous or shrubby groups, as well as their typically rather specific pollination relationships, should provide ideal conditions for rapid evolutionary differentiation, even under stable climatic conditions. There is some evidence that speciation in these groups frequently involves such phenomena as polyploidy (e.g., *Psychotria,* Hamilton, pers. comm.), hybridization (e.g., *Fuchsia,* Berry, 1980) or cleistogamy (e.g., Marcgraviaceae, Bedell, pers. comm.), Microgeographic, perhaps even more or less sympatric, speciation is probably

the rule rather than the exception. Shifts in specific pollinators are a common mode of speciation and co-evolution giving rise to finer biotic tuning of precise plant-pollinator systems such as those in *Heliconia* (Stiles, 1975), Orchidaceae (Dodson, 1975), Ericaceae (Luteyn, pers. comm.) or *Fuchsia* (Berry, 1980) seems a major evolutionary theme. In such groups speciation would appear an altogether open-ended phenomenon without the slightest hint of any kind of ecological equilibrium or limits on species diversity.

The Neotropics are much richer in epiphytes than the Palaeotropics (Richards, 1973; Madison, 1977; Burger, 1980). However, the tendency has been to explain this difference as due to lack of extinction in the relatively (at least to Africa) constantly mesic Neotropics and to interpret high epiphyte diversity as reflecting a long history of mesic conditions (Burger, 1980). I propose that high diversity in epiphytes and other Northern Andean-centered groups results mostly from recent very dynamic speciation, almost the antithesis of the prevalent lack-of-extinction hypothesis. Rather than the flora of tropical Africa (and to a lesser extent Asia) being impoverished with respect to the Neotropics, the latter may be considered as uniquely and phenomenally enriched.

There is increasing circumstantial evidence that this kind of unusually rapid speciation, concentrated along the base and lower slopes of the northern Andes, has involved much co-evolutionary interaction and has not been restricted to plants. Thus Stiles (1981) has shown that there are over 400 species of flower-feeding birds in the Neotropics, including 315 species of hummingbirds alone, as compared to 100–150 flower-feeding species in each Palaeotropical realm. Moreover, the Neotropical flower-feeding birds are generally much more specialized and show much greater flower specificity than their Palaeotropical equivalents. Stiles (1981) suggested from these patterns that bird-flower coevolution probably began relatively earlier in the New World than elsewhere. However, in the context of the botanical patterns discussed in this paper, I would suggest instead that it is probable that bird-flower coevolution, in general, and hummingbird speciation, in particular, has been much more rapid in the Neotropics. Certainly hummingbirds are concentrated in tropical and premontane parts of the northern Andean region (134 species in Colombia, ca. 133 in Ecuador (Bleiweiss, pers. comm.), 97 in Venezuela, 118 in Peru (Parker et al., 1982), compared to 52 in Panama (Ridgely, 1978), 51 in Costa Rica, 37 in Guatemala (Land, 1970), 60 in Mexico; see Stiles, 1981, table 5, for ecological and altitudinal distributional patterns) exactly as are the Andean-centered, largely hummingbird-pollinated groups of plants.

Although the data for flower-visiting bats are less precise, the rather generalized distributional patterns shown by Koopman (1981), are clearly similar to those of flower-visiting birds and my Andean-centered plant taxa. The greatest concentrations of nectar-feeding bat species (13 species each) are in the northern Andean region and Central America.

It is not yet clear whether such patterns are more a cause or an effect of the apparent evolutionary explosion of plant taxa characteristic of the northern Andean region. However, Terborgh and Winters (1982) have shown that for birds in general, local endemism is strikingly concentrated on the western side of the northern Andes, and Keister et al. (1983) have suggested theoretical reasons why

the partitioned population structures prevalent in this geographical region should favor rapid coevolution. Moreover, Marshall et al. (1982) note a grossly similar pattern for mammals with formation of the Isthmian land bridge resulting in what they consider to have been a balanced exchange of equilibrium faunas between North and South America followed by a unique and unbalanced secondary diversification of the immigrant taxa in South America, apparently somehow associated with the Andes. Perhaps the accelerated rates of speciation here suggested for northwestern South American plants is part of a much more general phenomenon.

To summarize, the exceedingly dynamic, even explosive evolution that seems to characterize the northern-Andean-centered taxa has given rise to a very significant proportion of the total Neotropical flora. Almost half of all Neotropical plant species appear to belong to these groups of epiphytes, understory shrubs, and palmettos, all of which are much more poorly represented in the Palaeotropics. Thus the historical accident of the Andean uplift, with the concomitant opportunity for explosive speciation among certain taxa of Gondwanan plants having the evolutionary potential for exploiting epiphytic, palmetto, and understory shrub strategies, may largely explain the "excess" plant species diversity of the Neotropics. It is essentially this *approximately half* of the Neotropical flora that is missing in the Palaeotropics, although similar patterns on a smaller scale might be expected in New Guinea, which seems the closest Palaeotropical equivalent of the Andean cordilleras.

Conclusion

A rich angiosperm flora similar to that in the rest of the tropics evolved during the last half of the Cretaceous in South America but this flora has subsequently given rise to many more species in the Neotropics.

At the end of the Cretaceous there was a possibility for relatively direct floristic interchange between South America and tropical North America via island hopping along the proto-Antilles; many of the Neotropical groups, especially some of the dry area taxa that show strong differentiation in both regions, may reflect this early interchange.

Uplift of the Andes, mostly in Neogene time, led to an incredible burst of speciation in a number of Gondwanan families. A similar evolutionary explosion in the same taxa also took place in Costa Rica and Panama. The taxonomic groups that have undergone this evolutionary explosion have distributional centers in the northern Andean region and southern Central America, are poorly represented in Amazonia, and consist mostly of epiphytes, shrubs, and palmettos; their pollination systems suggest that coevolutionary relationships with hummingbirds, nectar-feeding bats, and perhaps such specialized bees as Euglossines, have played a prominent role in their evolution. The evolutionary phenomena associated with the Andean uplift account for almost half of the total Neotropical flora and are thus largely responsible for the excess floristic richness of the Neotropics.

Closing of the Panamanian isthmus in the Pliocene led to (1) southward migration of some Laurasian taxa into the Andes where they have become ecologically dominant despite undergoing little speciation, at least in woody taxa, and

(2) northward invasion of lowland Gondwanan taxa of canopy trees and lianas into Central America, leading to their ecological dominance in lowland tropical forests throughout the region, despite little significant speciation in Central America.

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A REVIEW OF THE PHYTOGEOGRAPHIC EVIDENCES FOR PLEISTOCENE CLIMATE CHANGES IN THE NEOTROPICS[1]

GHILLEAN T. PRANCE[2]

ABSTRACT

A review is given of the various botanical evidences for changes in vegetation cover of the Neotropics during the Pleistocene dry periods. Authors who have discussed vegetation changes in terms of plant geography are treated. There are considerable phytogeographic data which support the findings of palynology and geomorphology. The climate changes appear to have affected the vegetation of the entire neotropical region since evidence is presented from Mexico to Southern Brazil and from both the lowland and highland regions. The comparatively recent recognition of climatic and related vegetational changes have caused botanists to re-evaluate some of their earlier theories of speciation and biological diversity in the lowland tropics.

INTRODUCTION

The refuge theory proposes large changes in the vegetation cover and plant species distributions of the lowland tropics during the Pleistocene and Holocene. The theory was developed in the Americas by a zoologist (Haffer, 1969) and since then many other zoologists have also furnished zoogeographic evidence. Considering the implications of the refuge theory for botany there have been few papers about refugia by botanists based on plant distributions and vegetation types. Consequently there is a relatively small literature base about plants and refugia. However, the changes in plant distribution and vegetation types are obviously basic to the refuge theory. The lack of botanical papers about refugia is partially due to the inadequate specimen sample from the region. Only two botanists have proposed locations of refugia over an extended area. The highland areas of South America have been studied in some detail (B. Simpson, 1975, 1978). The lowland refugia of Haffer (1969) were discussed and modified slightly in light of plant distributions by Prance (1973, 1981a). There are, however, several discussions of refugia for smaller areas such as Mexico and adjacent Central America by Toledo (1976), Chocó in Colombia by Gentry (1981), and Venezuela by Steyermark (1979, 1981).

Until recently botanists explained plant speciation in the lowland tropical rain forests under the assumption that the forest had remained stable over a long period of geological time (e.g., Federov, 1966; Ashton, 1969; Richards, 1969). Only recently have botanists come to recognize that this presumed stability of the forest was not necessarily the case, and that quite recent changes in climate

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must be considered as an important factor in plant geography, in speciation, and as a cause of extinctions.

The new emphasis on the instability of the rain forest vegetation in the Pleistocene and post-Pleistocene period does not necessarily eliminate the importance of some of the other models of plant speciation. For example, in the Amazonian rain forest habitat there are an enormous number of niches available and the niche speciation emphasized by Richards (1969) and Ashton (1969) is likely to be important for the speciation of forest trees and vines. The competition and interaction with pollinators has led to phenological separation, there is separation of closely related species into different strata of the forest, and species pairs with one in the inundated forest and another in the forest on terra firme are common. The danger of discussing any one theory such as refugia is that the other models of speciation will be ignored. However, it now appears that refugia have been one of the most important causes of plant speciation and therefore of species diversity of Amazonia, but the discussion below assumes that other methods of speciation are also important.

Botanical evidence for climate changes in the Pleistocene is based largely on chorological data obtained by mapping plant distributions in order to pinpoint centers of endemism in the lowland forest areas and to indicate patterns of disjunct distribution. Some zoologists have used other techniques. For example, the statistical analysis of geographic variation in lizards (Vanzolini & Williams, 1970) or the genetic analysis of hybrid zones in butterflies (Brown, 1976, 1979; Turner, 1976). Below I have summarized the published botanical evidence for refugia excluding palynology, which has been extensively reviewed elsewhere (e.g., Absy, 1979; van der Hammen, 1974, 1981). Pollen provides the most definite botanical evidence of Pleistocene climate changes in the Neotropics upon which authors have been able to interpret their phytogeographic data. These data are backed up by considerable evidences from geomorphology, for example, by Ab'Sáber (1977), whose map for 18,000 B.P. is shown in Fig. 1. Here I will consider mainly the plant distributional evidences for changes in the vegetation cover of the Neotropics in the Pleistocene. It is now possible to interpret some of the unusual distribution and clusters of endemics because there is a growing quantity of solid evidence from geomorphology and palynology. Much of this is summarized in various papers in Prance (1981b).

Andean Region

Vuilleumier (1971) was the first botanist to comment on the refuge theory in South America. Her paper was a general review of the geological and palynological evidence for the refuge theory and it also presented considerable details about glaciation in the Andean highlands and the southern tip of South America. The review was based mainly on the speciation patterns of high Andean plant and avian taxa, and the lowlands were not discussed in detail. Although written by a botanist, this paper presented no really new botanical evidences. Attention was drawn to the relationship of the flora of the Venezuelan highlands with that of the plateau of Central Brazil, and to the distribution pattern of the genus *Polylepis* (Rosaceae) in the Andes. The distribution of this genus, which forms

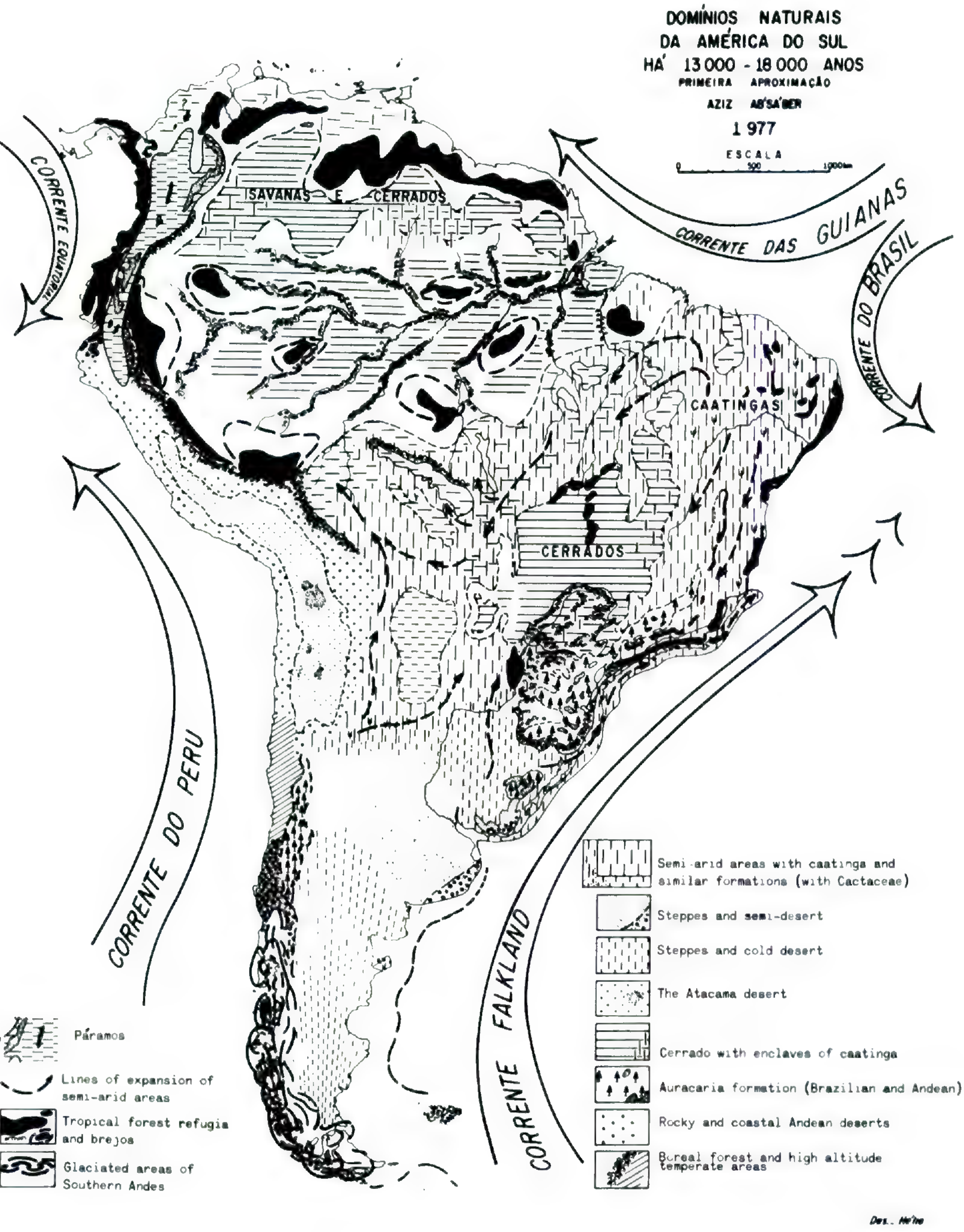

FIGURE 1. The vegetation of South America 13,000–18,000 B.P. as proposed by Ab'Sáber. The black areas are proposed forest refugia, most of the rest of Amazonia is shown as savanna, cerrado, and caatinga, all vegetation types characteristic of drier climate than that of present day Amazonia (from Ab'Sáber, 1977).

distinct isolated patches of woodlands at higher elevations in the Andes, is consistent with a sequence of humid-arid changes in climate along the Central Andean slopes where the tree line changed several times. In a later paper, B. Simpson (1975) presented her botanical evidences in detail. This paper also dealt exclusively with the high tropical Andes, and described the changes during the Pleis-

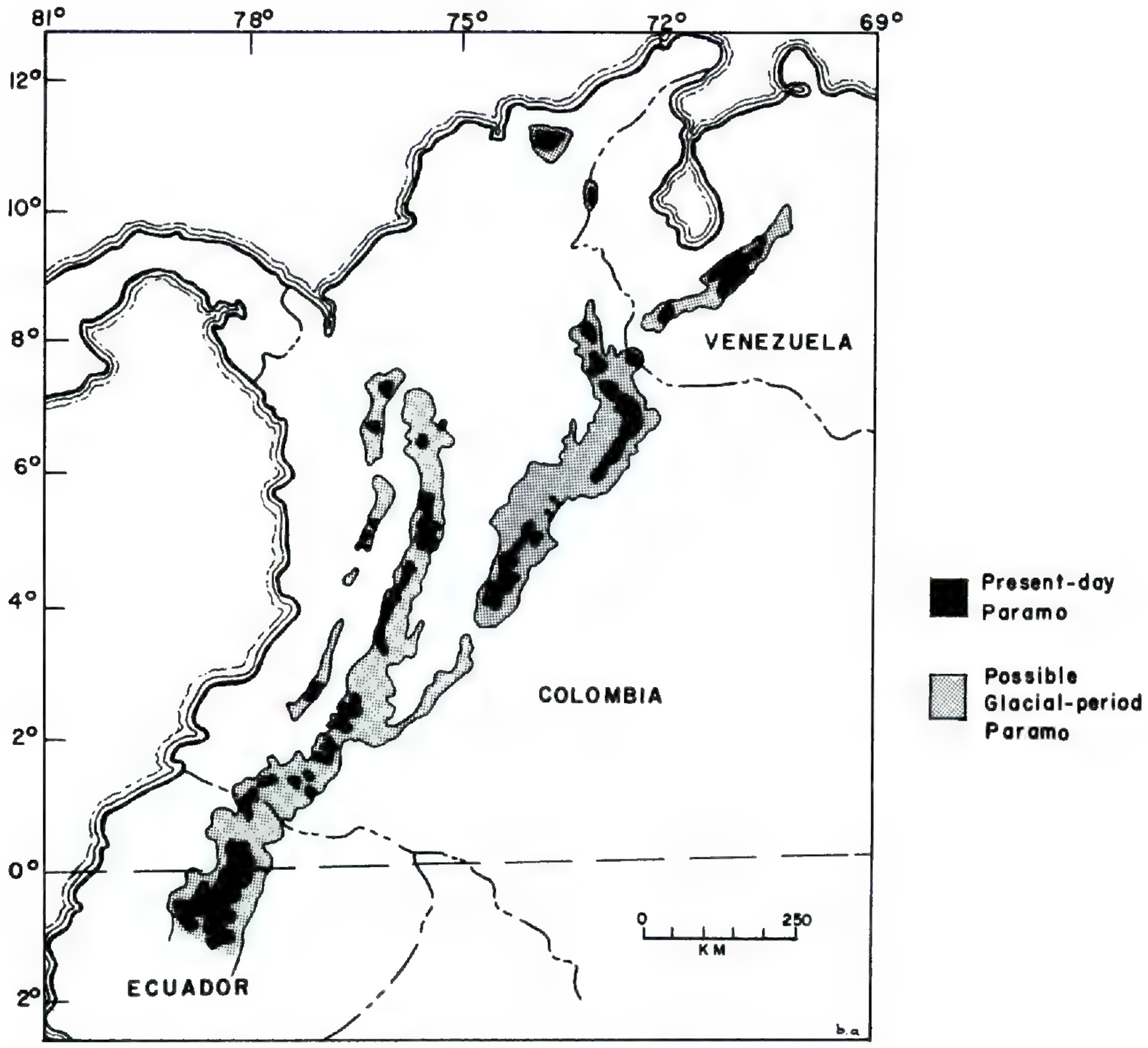

FIGURE 2. The distribution of Páramo vegetation: Present day represented by black areas and Pleistocene maximum glaciation period by gray area, estimated by lowering the altitude by 1,000 m (after van der Hammen, 1981). The black areas also include all areas above the páramo with permanent snow and glaciers.

tocene of the flora at altitudes of over 3,000 m to the páramo of the northern Andes, the puna of the Altiplano, the upper Andean forests, and the dry desert scrub of the high intermontane valleys. Simpson also included a good review of the history of the uplift of the Andes and the gradual availability of the various different Andean habitats for plant colonization. Since most of these habitats have become available primarily in the Quaternary or only the late Tertiary, they are intimately connected with the vegetation of the lowlands. Simpson found an altitudinal and latitudinal variation in the way plant species moved into the Andean habitats, the manner of differentiation during the Pleistocene, and the time of immigration into their habitat. Speciation appears to have taken place mainly through geographic isolation caused by the various changes in vegetation distribution during the Pleistocene and Holocene. With the exception of the Altiplano, most species expanded their ranges when the lowering of the high altitude habitats occurred during the Pleistocene cool periods. For example, in the northern páramos the greatest colonization was during the glacial periods in a manner similar to Oceanic islands. At the lower elevation in the northern Andes of the eastern Cordillera direct migration was possible (Fig. 2). The interglacial periods, which occurred several times, were times of isolation and differentiation. In contrast,

in the Altiplano the glacial periods were times of population fragmentation accompanied by differentiation and/or speciation.

Simpson distinguished two elements in the páramo flora: 1) species groups which are not closely related to lowland groups, and 2) species groups which are closely related to lowland groups. It is the latter that are of interest for the study of the history of the lowland Amazon flora. An analysis of the high Andean flora shows that it was colonized in a way analogous to oceanic islands because there are significant correlations between areas of páramo and their distances from source areas and the number of plant taxa which now inhabit them. There is an even stronger correlation with glacial period parameters and páramo size which suggests that the majority of colonization occurred in glacial periods when plant propagules were able to disperse more easily because of increased size of the páramos.

These highland Andean data together with much palynological work have proved undisputably that there were considerable changes in the highland South American flora during the glacial periods. The changes in páramo in the extreme highlands meant changes in cloud forest and mountain slope forest at lower altitudes. The importance of the slope forest as a possible migration route for plant species must be considered in a discussion of the lowland forest. The details of the lowland flora have not been worked out in such detail as those of the highlands. An interesting part of the highland work is the comparison with and use of some of the concepts of island biogeography which are an integral part of the refuge theory.

FOREST REFUGIA IN THE LOWLANDS

The lowland areas of Amazonia and the refuge theory have been commented upon by various taxonomic botanists from their experience with the groups of plants in which they specialize.

D. R. Simpson (1972), in a paper which was published only in abstract form, studied the distribution patterns of some Amazonian species of Rubiaceae. He observed that these distributions support Haffer's theory for the Peruvian part of Amazonia particularly confirming a floristic difference between the Napo refugium and the east Peruvian refugium further to the south. The most interesting part of Simpson's work was to point out some of the xeromorphic features of trees of the humid forest of Peru. He used these as evidence that xeromorphic traits must have evolved in a xerophytic or subxerophytic climate. He proposed that these species with xeromorphic adaptations are relicts from gallery forests and forest islands which formerly existed in the midst of savannas.

This is an interesting idea. However, there are many present day habitats in Amazonia where xeromorphic adaptations are an advantage such as white sand campinas, black water igapós, and rock outcrops which still offer dry season xerophytic habitats in lowland Amazonia under present day climate conditions. These could also produce xeromorphic adaptations which were retained after the migration of the species into the rain forest. However, such migration is not as likely as that caused by the now well documented climate changes, and subsequent expansion and contraction of forest.

Tryon (1972) discussed centers of endemism and geographic speciation in

tropical American ferns. He pinpointed centers of endemism without any reference to the refuge theory. Centers of endemism are Mexico, the Andes, and southeastern Brazil, with secondary centers in Central America and the Guianas. The intervening, mainly lowland areas are less distinctive in terms of their fern species and tend to have widely disturbed common lowland species. The centers of endemism are important as areas of speciation, species persistence, and as sources of material for migration. Tryon proposed that migration through intervening areas between his centers of endemism occurred both during past climatic changes by continuous dispersal, and by long distance dispersal. He also discussed speciation by isolation after long distance dispersal or loss of continuous distribution.

It is hard to draw any conclusions about lowland tropical areas from this work because ferns thrive at the cooler, higher altitudes and the centers represent this more suitable climate, and also because long distance dispersal is easy for relatively light fern spores. However, it is apparent that the areas of endemism for the ferns must have had stability for a long time and we can look to those areas as a possible source of other plant material for migration into the lowland areas. It is interesting that the lowland ferns do not apparently show regional diversification as a result of the forest refugia; probably this is due to their easy dispersal and relative paucity of fern species in the lowland tropical moist forest.

Langenheim et al. (1973) made an ecological and evolutionary study of the lowland Amazonian species of the Caesalpiniaceous genus *Hymenaea*. They discussed five Amazonian rainforest species together with their relatives in drier habitats and in the Atlantic coastal forest of Brazil. They considered *H. eriogyne* Benth., which occurs in forest islands in the caatingas of northeastern Brazil, and the two species of the Atlantic coastal forests (*H. rubiflora* Ducke and *H. aurea* Lee & Langenh.) as relicts from early Tertiary times when Amazon forest had a more southerly distribution. These species are relicts which have found refugia in eastern Brazil, *H. aurea* in the upland forest of Bahia and *H. eriogyne* in the forest patches within the drier caatinga. Langenheim et al. gave a brief review of evidences for Pleistocene forest changes and accepted them as fact.

Hymenaea shows adaptive radiation from humid rain forest to a variety of drier ecosystem types which they proposed initiated in the mid-Tertiary and continued into the Pleistocene. The authors discussed the habitat and adaptations of each species of the genus. The presence of *H. oblongifolia* Huber var. *palustris* Lee & Langenh. in Chocó, Colombia is said to indicate a more widespread distribution of this species in the past. *H. courbaril* L. var. *subsessilis* occurs on sandy beaches and tributaries of Central Amazonia, and its small tree form is postulated to have developed during the long interval of the Pleistocene. This is not necessarily so because sandy beaches are a present day habitat and one would expect various species to adapt and occupy this niche even without the stimulation of drier periods. The sandy beaches of Central Amazonia have many distinct species or forms of forest species with a smaller stature.

Langenheim et al. stated that "although present evidence regarding speciation within Amazonian *Hymenaea* does not clearly support the hypothesis of dry oscillations during the Pleistocene, it does not negate the possibility." They in-

dicated that there was definite evidence from *Hymenaea* that evolution had responded to dry environmental conditions. *Hymenaea* also demonstrates that the Amazonian hylaea of today is not a vast uniform habitat, but a heterogeneous mixture of seasonally dry forest, savanna, campina, and caatinga, as well as moist forest. The authors questioned the idea of refugia being small peripheral islands as suggested by Vanzolini and Williams mainly because the regeneration of tropical rain forest is slow, and studies demonstrate the slow rate of recolonization of large agricultural areas. These authors felt that the ecology of rain forest trees and their slow invasion of savanna types suggested that relatively large areas of hylaea remained even during the Pleistocene dry climate periods. This is more in agreement with some recent papers on refugia which have tended both to enlarge the area and number of refugia and to emphasize that the area between refugia did not necessarily all become the kind of open savanna we know today, but rather was often an impoverished forest with a reduced species density.

Moore (1973) in a discussion primarily concerned with the worldwide distribution of palm genera, commented briefly on the Pleistocene and recent history of the palms of Africa and South America. He mentioned that the more drastic Pleistocene changes in Africa in comparison with South America were the reason for the depauperate palm flora of Africa (16 genera, 117 species from 7 major groups in Africa compared with 64 genera, 837 species from 9 groups in South America). Moore accepted the data of Haffer (1969) and Vuilleumier (1971) and discussed palms from that assumption. Moore had species data available for only a few palm groups such as *Pholiodostachys* and *Geonoma* section *Taenianthera* which seemed to offer a certain amount of support to the refuge theory. This evidence was based on the disjunct distribution of four genera: *Phytelephas*, which occurs in the Panama-Catatumbo refugia and is disjunct in east Peru; *Wettinia* in Chocó and east Peru; *Chelyocarpus* in Chocó and south Peru and Rondônia; and *Orbignya* section *Spirostachys* in Chocó and around Leticia in Amazonian Colombia. From these distributions Moore pointed out the clear relationship between Haffer's east Peruvian and Napo refugia with the Chocó refugia where identical or vicarious species occur. Moore also observed, however, that some species of palms such as the ubiquitous *Mauritia flexuosa* L., *Euterpe precatoria* Mart., *Socratea exhorrhiza* (Mart.) Wendl., *Maximilliana martiana* Karst., and *Geonoma deversa* (Poit.) Kunth had been eminently successful either in persisting through change or in redispersing. He also discussed the converse of forest reduction and the present day distribution of some palms of dry areas. The present day distribution of some palms such as some Cocosoid palms, species of *Syagrus* and *Orbignya*, was explained by the fact that the range had been of even greater extent in the past. Moore also reviewed the earlier history and origin of the palms and its possible influence on the more recent history.

I would make two comments on Moore's ideas. Firstly, the evidences he uses for refugia mainly concern the relationship between Chocó and eastern Peru, i.e., a trans-Andean relationship. Undoubtedly, both these areas were stable refugia during the Pleistocene and the palms cited are some of the examples of such a relationship. However, the species were probably isolated earlier by the uplift of the Andes rather than by the Pleistocene climate changes and have not since been

able to coalesce. Chocó is most important as a Pleistocene refugium, but in the case of plants it is much less important as a center of material for redistribution to the other lowlands. Hence, it is a much older and isolated refugium than those which are situated east of the Andes. Secondly, several of the palm species cited above, such as *Mauritia flexuosa* and *Socratea exhorrhiza*, are characteristic of wet places such as gallery forests and swamps. They probably persisted with a wide but only slightly reduced distribution during the Pleistocene, surviving in the gallery forests of rivers much as they do today in the gallery of savanna areas.

Prance (1973) studied the distribution patterns of Amazonian Caryocaraceae, Chrysobalanaceae, Dichapetalaceae, and Lecythidaceae, all families of woody angiosperms with their Neotropical distributions centered in Amazonia. This study pinpointed centers of endemism in the lowland forest, discussed morphologically variable widespread species and disjunct distributions such as that of *Stephanopodium* (Dichapetalaceae), which is distributed in northern South America and eastern coastal Brazil. Nineteen maps showed the distribution of several of the species studied. An attempt was made to locate possible refugia and to interpret those of Haffer (1969) in terms of the distribution patterns of forest trees. Prance agreed with the following refugia of Haffer: Chocó, Nechi, Catatumbo, Northern Venezuela (Rancho Grande), Guiana, Imerí, Napo, Eastern Peru and the Madeira-Tapajós refugium (moved slightly westward and called Rondônia-Aripuanã), and Belém-Xingu. Additional refugia were proposed at Paria and Imataca in eastern Venezuela, Olivença and Tefé in the western part of Brazilian Amazonia, and north of Manaus in Central Amazonia (see Fig. 3). This paper also stressed the importance of gallery forests both as refugia and as contact areas during the drier periods. This was compared with the many Amazonian present day forest species which are distributed well into the Planalto of central Brazil by means of the gallery. This paper is the only one so far by a botanist which has sought to map refugia over the entire lowland area. Prance did not consider the Atlantic coastal refugia of eastern Brazil in any detail apart from suggesting that the area is an area of refugia.

In later papers Prance (1978, 1981a) reviewed briefly the botanical data which has been used to discuss refugia, and presented another map of refugia (Fig. 4), which was not greatly different from that of Prance (1973) except to place a greater emphasis on the role of the gallery forests during the Pleistocene. The papers discussed the species diversity of the Amazon forest giving examples from inventories and citing an example of ten sympatric species of *Eschweilera* (Lecythidaceae) on the same hectare of terra firme forest near to Manaus. They also discussed the present day distribution of savannas in Amazonia and the role of gallery forest and forest islands in savanna. The following disjunctions were observed: between Panama and Guiana, for example *Licania affinis* Fritsch (Chrysobalanaceae); between Guianas and western Amazonia, for example *Mouriri oligantha* Pilg.; between Amazonia and Pernambuco, for example *Hirtella bicornis* Mart. & Zucc. and the species cited in Andrade-Lima (1953); between Amazonia and Rio de Janeiro, for example *Couratari macrosperma* A. C. Smith (Lecythidaceae) and between northern South America and eastern Brazil, for example the genus *Stephanopodium*. These disjunctions were explained in terms of changes in forest cover rather than long distance dispersal. These papers also

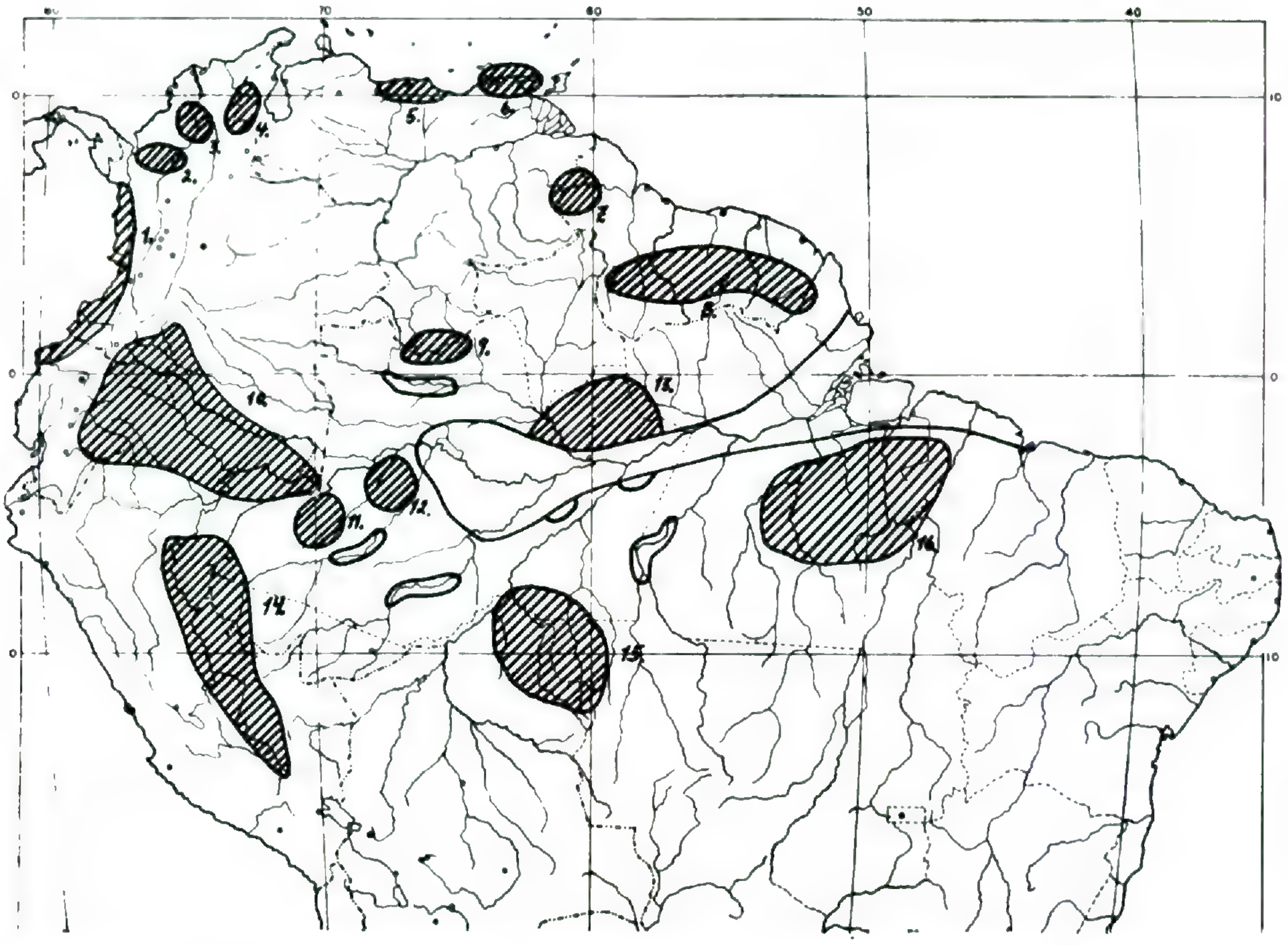

FIGURE 3. The forest refugia proposed by Prance (1973) from a study of endemism in forest species of four woody plant species: 1, Chocó; 2, Nechi; 3, Santa Marta; 4, Catatumbo; 5, Rancho Grande; 6, Paria; 7, Imataca; 8, Guiana; 9, Imerí; 10, Napo; 11, Olivença; 12, Tefé; 13, Manaus; 14, East Peru; 15, Rondônia-Aripuanã; 16, Belém-Xingú.

discussed polymorphic species (ochlospecies) and reasons for their variation and finally centers of species diversity in the lowland forests were identified.

Soderstrom and Calderón (1974) studied the tribes of bambusoid grasses Olyreae and Parianeae, especially the genera *Diandrolyra* and *Piresia* both of the former tribe. They found that the primitive species of the group occur in the forests of eastern Brazil, particularly in Bahia and north of the Rio Doce in Espírito Santo. They hypothesized that eastern Brazil, particularly Bahia, represents a refugium of the primitive elements of these genera and that migration occurred south along Serra do Mar and northwest into Amazonia. The forest area from Bahia north to the State of Paraíba is considered a refugium for at least some primitive herbaceous bambusoid grasses. They commented briefly that Amazonia was also populated from the north where the Panamanian-Chocó refugium harbors such primitive grasses as the Olyroid genus *Maclurolyra*.

The distribution of *Piresia* of the Olyreae would certainly support the Bahia refugium theory well. *Piresia* has four species in Bahia and one species in the refugium of Peruvian Amazonia as well as two species which are widespread in northeastern Amazonia and are sympatric in the Guiana refugium area.

Further evidence for a Bahia refugium and other refugia in Atlantic coastal Brazil is given in Mori et al. (1981), which is a study of the distribution of 127 species that occur in the region. Fifty-three and one-half percent of the

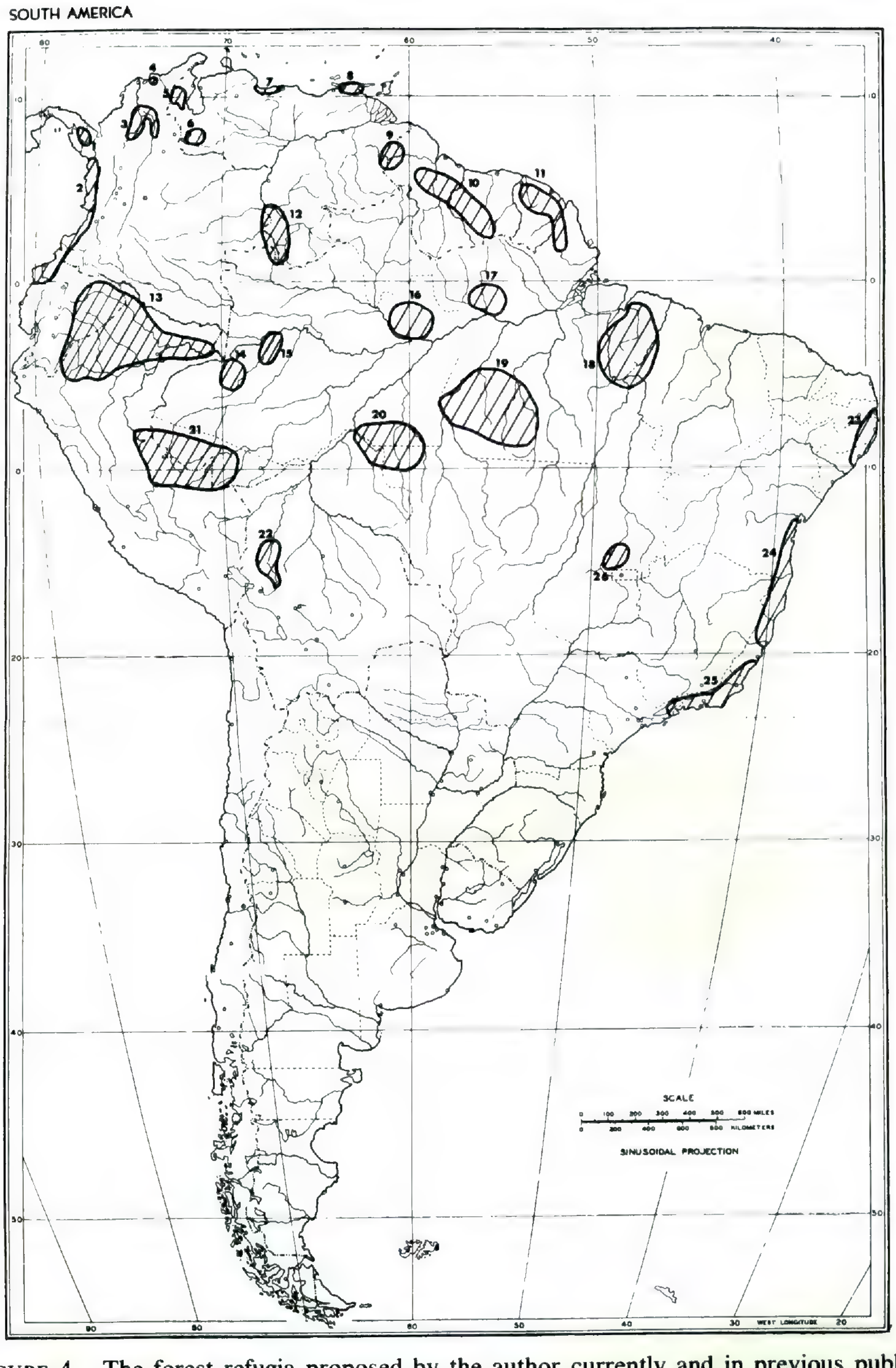

FIGURE 4. The forest refugia proposed by the author currently and in previous publications (Prance, 1978, 1981a): 1, Panama-Darién; 2, Chocó; 3, Rio Magdalena; 4, Santa Marta; 5, Catatumbo; 6, Apure; 7, Rancho Grande; 8, Paria; 9, Imataca; 10, West Guiana; 11, East Guiana; 12, Imerí; 13, Napo; 14, Olivença; 15, Tefé; 16, Manaus; 17, Trombetas; 18, Belém; 19, Tapajoz-Xingu; 20, Airpuanã; 21, E. Peru-Acre; 22, Beni; 23, Pernambuco; 24, Bahia; 25, Rio-Espírito Santo; 26, Araguaia.

TABLE 1. Analysis of 31 species of Memecyleae considered as local endemics by Morley (1975), showing relationships to refugia and habitat, see also Figs. 5 and 6. The refugia of Haffer (H), Vanzolini (V), and Prance (P) are referred to by Morley, and for the Atlantic coast the Serra do Mar dispersal of Müller (M) is used.

A. Endemic species which according to Morley (1975) fit proposed refugia.

	Refuge	Authors	Habitat Data
Mouriri pseudogeminata Pittier	N. Venezuela	HVP	Open deciduous forest
rhizophoraefolia (DC.) Triana	Imataca (near)	P	Forest
micranthera Morley	Chocó	HP	Forest
pachyphylla Burrett	Chocó (+ Gorgona Is.)	HP	Forest
angustifolia Spruce ex Triana	Imerí (near)	HP	Moist caatinga
spruceana Morley	Imerí	HP	Caatinga & disturbed forest
duckeanoides Morley	Manaus	P	Forest on terra firme
froesii Morley	Manaus (near)	P	No data
Votomita pleurocarpa (Morley) Morley	Olivença (near)	P	Forest on terra firme
monadelpha (Ducke) Morley	Belém	HP	Forest on terra firme
orbinaxia Morley	Belém	H	Forest on terra firme
Mouriri obtusiloba Morley	Belém (near)	P	No data
arborea Gardn.	Serra do Mar	M	Forest
doriana Morley	Serra do Mar	M	Forest
chamissoana Cogn.	Serra do Mar	M	Forest
bahiensis Morley	Serra do Mar	M	Forest
regelliana Cogn.	Serra do Mar	M	No data

B. Endemic species which "fit none of proposed refugia" (fide Morley, 1975).

		Habitat Data
Mouriri francavillana Cogn.	Guiana, near coast outside refugium	Forest on terra firme
Votomita guianensis Aubl.	Guiana, near coast outside refugium	Forest on terra firme
Mouriri ambiconvexa Morley	W. Amazonia, Colombia, Rio Apaporis	No data
barinensis (Morley) Morley	Venezuela, Barinas, Ticoporo	Wet forest
dimorphandra Morley	Central & S. Amazonia, Manaus-Porto Velho	Forest on terra firme
eugeniaefolia Spr. ex Tr.	Central & W. Amazonia, Manaus-Rio Vaupés	Igapó
exadenia Morley	Peru, Loreto: Rio Huallaga	Dense forest
floribunda Markgraf	Peru, Amazonas, Pongo de Manseriche	Forest on terra firme
longifolia (HBK) Morley	Venezuela, Amazonas	Moist forest
micradenia Ducke	Brazil, São Paulo de Olivença	Forest on terra firme
monopora Morley	Brazil, Amazonas, Ig. Jandiatuba	Forest on terra firme
tessmannii Markgraf	W. Amazonia, Peru, Pongo de Manseriche	Forest on terra firme
uncitheca Morley & Wurdack	Venezuela, Amazonas	White sand scrub
orinocensis Morley	Venezuela, Amazonas, Río Orinoco	Bank of river

forest species are shown to be endemic there and the distributions indicate a clear separation of a northern and southern refugium in the region. The region of Rio de Janeiro has many endemics that separate it from that of southern Bahia-northern Espírito Santo which is another area of high endemism.

Morley (1975) has made the most detailed, botanically based, critique of the refuge theory based on the distribution of species of Memecyleae (Melastomataceae). Morley argued that present day climate distribution could account for the distribution of all species of the group except *Mouriri oligantha* Pilg. He favored habitat preference and tolerance ranges over climatic variations as the cause of speciation in the Memecyleae. However, he cited several other cases in his paper which fit well into the refuge theory. Since the Memecyleae are a woody group primarily of forest, and are well worked out taxonomically with readily recognizable species as defined by Morley, they are discussed in some detail here. Morley's discussion is based on the refugia proposed by Haffer (1969), Vanzolini and Williams (1970), and Prance (1973).

FIGURE 5. Distribution map of Memecyleae (Melastomataceae) which according to Morley (1975) fit well into refugia: a, *Mouriri panamensis*; b, *M. micranthera*; d, *M. pachyphylla*; e, *M. rhizophoraefolia*; f, *M. froesii*; g, *M. angustifolia*; h, *M. spruceana*; i, *Votomita pleurocarpa*; j, *Votomita monadelpha*; k, *Mouriri duckeanoides*; n, *V. orbinaxia*; o, *Mouriri chamissoana*; p, *M. obtusiloba*; q, *M. bahiensis*; r, *M. regeliana*; s, *M. arborea* and *M. doriana*; t, *M. pseudogeminata*.

Table 1 is an analysis of 31 species of Memecyleae which are listed by Morley as local endemics, and these species are also mapped in Figs. 5 and 6. There are 17 species which fit near to the refugia discussed (Fig. 5), and 14 local species which, according to Morley, do not fit well into the refugia (Fig. 6). The 14 local species which do not fit according to Morley need to be considered further. Eleven of these species occur quite near to the refugia of Prance (1973) and only three are completely outside refugium areas: *M. eugeniaefolia* Spruce ex Triana, a species of black water igapó with a typical distribution on the Rio Negro of many species adapted to that habitat; *M. ambiconvexa* Morley, a species without habitat data, but probably of white sand caatinga; and *M. dimorphandra* Morley, a rain forest species with rather a wide distribution from the Manaus refugium area south to Porto Velho in the Rondônia refugium. The first two species are adapted to specific habitats other than the rain forest and cannot be used as evidence for or against refugia, but show one of the other types of speciation

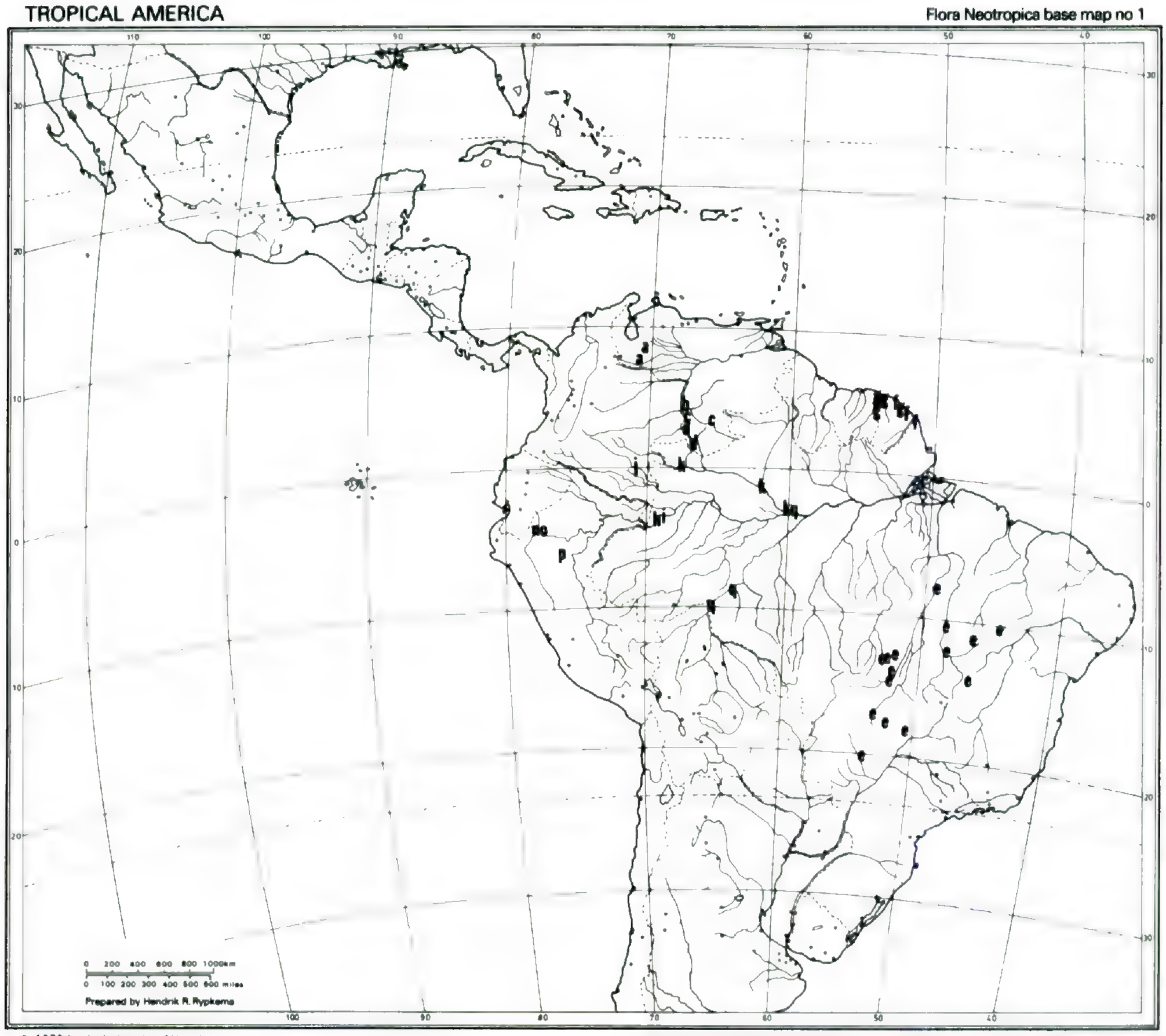

FIGURE 6. Distribution map of Memecyleae (Melastomataceae) which according to Morley (1975) do not correspond well to refuge theory, and *M. elliptica* of Central Brazil: a, *Mouriri barinensis*; b, *Votomita orinocensis*; c, *Mouriri longifolia*; d, *M. uncitheca*; e, *M. elliptica*; f, *M. francavillana*; g, *Votomita guianensis*; h, *Mouriri micradenia*; i *M. monopora*; j, *M. ambiconvexa*; k, *M. eugeniaefolia*; n, *M. tessmannii*; o, *M. floribunda*; p, *M. exadenia*; q, *M. dimorphandra*.

which occurs, adaptation to present day habitats. Nine of the other eleven endemic species said to fall outside refugia are forest species and must be considered in the studies of refuge theory, and two are local habitat adaptations (*M. uncitheca* Morley & Wurdack to white sand scrub of the Orinoco region and *Votomita orinocoensis* Morley to rocky riverine habitats of the Rio Orinoco). The nine forest species are discussed individually below:

1. *M. barinensis* Morley is southwest of the Catatumbo refugium of Prance (1973) and nearer to the Apure refugium of Brown (1976), which is recognized here.

2. *M. longifolia* (HBK) Morley is north of the Imerí refugium of Prance (1973) and within the Ventuari refugium of Brown (1976), and the Imerí area as redefined here.

3. *M. guianensis* Aubl. and *M. francavillana* Cogn. are distributed just north

of the Guiana refugium of Prance (1973), Brown (1976), and within the area designated as the Guiana refugium in the present work.

4. *M. tessmannii* Markgraf and *M. floribunda* Markgraf are just south of the Napo refugium of Prance (1973) and Brown (1976). These two species occur at the Pongo de Manseriche, an area of high endemism which has been included in the Napo refugium as defined here.

5. *M. exadenia* Morley occurs very slightly outside the east Peru refugium of Prance (1973) in an area of relatively low botanical endemism.

6. *M. micradenia* Ducke and *M. monopora* Morley occur near to São Paulo de Olivença, Brazil, only slightly north of the Olivença refugium of Prance (1973), which has been moved in the present work to include the area where these two species occur.

The data from the endemic species of Memecyleae help to define refugia better through slight modification of earlier proposals rather than contradict the refuge theory. The data demonstrate centers of endemism and the possible location of refugia.

In addition to considering endemics, Morley discussed two species pairs and one disjunct species of *Mouriri* which are further supportive of the refuge theory. *Mouriri crassifolia* Sagot is a common species of the Guianas, Amapá, and eastern Pará, and its closest relative *M. ficoides* Morley is common around Manaus. The same distribution occurs in *M. dumetosa* Cogn. of the Guianas and *M. densifoliata* Ducke from around Manaus. These appear to be two vicarious species pairs and a logical explanation of their separation into two populations is by the changes in forest cover during dry periods.

Mouriri oligantha Pilg. is divided into two distinct populations, one in the Guianas and the other in eastern Peru. Morley proposed that this species had a continuous distribution at a time of greater humidity and was distributed around the embayment of Amazonia and was later broken into two populations by a drier climate cycle. This type of distribution in the Guianas and eastern Peru is paralleled in many other plant distributions (e.g., *Couepia parillo* DC, Chrysobalanaceae; *Tassadia guianensis* Decne, Asclepiadaceae, see Pereira (1977)), and is good evidence of the effect of drier phases in Central Amazonia.

In addition to the local and disjunct species mentioned above, *Mouriri* has three widespread polymorphic ochlospecies with much local variation throughout their range, *M. grandiflora* DC., *M. vernicosa* Naud., and *M. guianensis* Aubl., with their maximum differentiation in the Guianas. This variation can also be accounted for by adaptation to climate changes and will be discussed further below.

Although Morley argues that the present day climate differences could account for all the geography of *Mouriri* except *M. oligantha*, it seems that his data can be interpreted differently to show clear evidence of the effect of Pleistocene climate changes. Distribution patterns that correlate with present day climate do not negate the idea of Pleistocene refugia.

Sastre (1976) made a study of the open vegetation areas of the Guianas with particular attention to the savannas and mountain tops. He found that the Guiana savannas individually show no endemism, but that the sandstone mountains over

1,000 m in altitude show considerable endemism. He estimated that forty percent of the species of granite outcrop also occur in the lowland savannas, and that fifty-five percent of the species were confined to mountain tops. Of these fifty-five percent, forty percent are rock specific. He discussed the problems of the distribution of mountain top savanna species, which are often divided into populations separated by 300 km or more of forest. Sastre observed that long distance dispersal by birds answers some, but not all of these distributions and called on the spread of savanna in dry periods to explain some of these distributions. He also recognized the Guiana mountains as a center of species differentiation for species of open habitats because of their subsequent isolation as small islands of vegetation where differentiation between islands took place.

It is interesting to note that many species of savanna and other open areas have obvious adaptations for long distance dispersal in marked contrast to those of the rain forest. This limits the use of distribution data from savanna species to draw conclusions about savanna changes. For example, Macedo and Prance (1978) showed that 75.67% of species of Amazonian white sand campina have this capacity for long distance dispersal by birds but also bats or the wind.

Descamps et al. (1978) in part of the same study as Sastre (1976) worked on the plants and animals of savannas and rock outcrops of French Guiana. They divided the Guianas into three biogeographic subregions based on the distributions of various forest species. They concluded that speciation of forest species in the Guianas took place in more than one center and that during the times of dry climate the Guianas were broken up into at least three refugia rather than the single one proposed by Haffer (1969) and Prance (1973). They suggested that the easternmost refugium is located north of the Tumucumaque mountains between Tampoc and Camopi rivers around Saül and between the Comté and the Approuaque. This is farther northwest of the Oiapoque refugium of Brown (1976).

The most detailed refuge analysis for French Guiana is that of de Granville (1981). He postulated a large central refugium in the zone of the present day high rainfall where there is greatest vegetational diversity centered around Saül (Fig. 7). The refugium occupied most of central and eastern French Guiana with its northern limit in the Kaw range and southern one in the Inini-Camopi mountains and extending eastward into Amapá Territory of Brazil. He cited as evidence many interesting endemics from the region such as *Elephantomene eburnea* Barneby & Krukoff (Menispermaceae), and four different species of *Psychotria* (Rubiaceae). The Saül region also has a number of species, such as *Oedematopus octandrus* Planch. & Triana, which are widely disjunct in other areas and provide evidence of isolation. De Granville believes that on the basis of vegetation distribution that the later dry period of the recent Holocene (4,400–2,200 B.P.) also had an impact on the vegetation not by causing new savanna, but by delaying the advance of the forest.

De Granville also discussed remnants of an arid flora of French Guiana in today's humid climate. The arid vegetation is now separated into discrete isolated sites acting as refugia for the arid species. The arid vegetation type of three coastal savannas is of limited use for refuge study because it was flooded as recently as 6,000 years B.P. However, the rock outcrops (inselbergs) and emergent rocks in rivers are much older refugia for arid region species. De Granville provided fur-

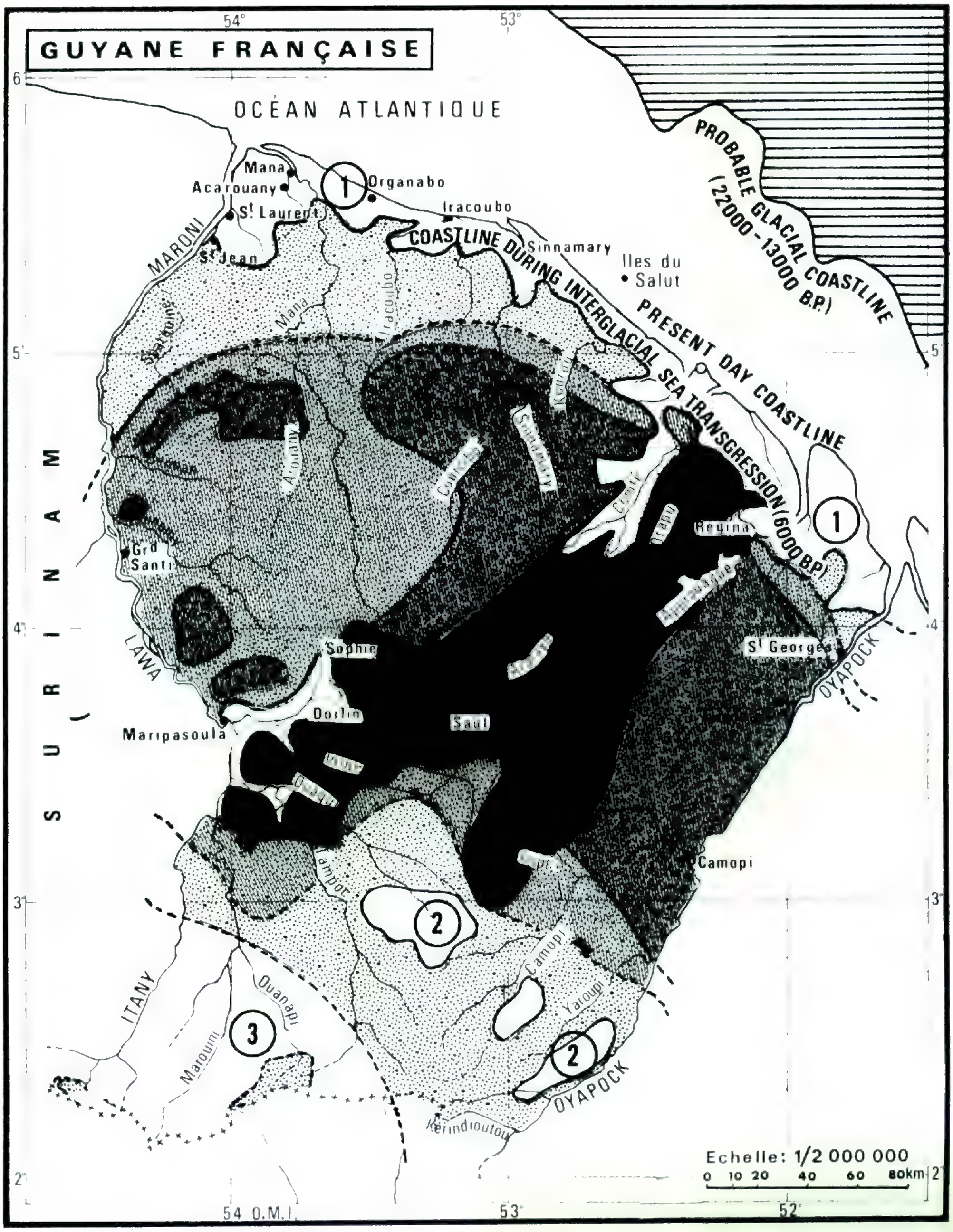

FIGURE 7. The Pleistocene forest refugium proposed by de Granville (1981) for French Guiana.

ther data about the vegetation outcrops of the Tumac-Humac region studied by Sastre (1976) and Descamps et al. (1978). Some of the arid adapted species are equally saxicolous, savannicolous, and of the coastal savannas, e.g., *Borreria latifolia* (Aubl.) K. Schum., *Stylosanthes hispida* Rich., and *Xyris fallax* Malme. Other species are confined to one of these arid vegetation types.

FIGURE 8. The distribution of *Trigonia* (Trigoniaceae) discussed by Lleras (1978) in connection with refuge theory: a, *T. sericea*; b, *T. sprucei*; c, *T. prancei*; d, *T. subcymosa*; e, *T. bracteata*; f, *T. villosa* var. *macrocarpa*; g, *T. coppenamensis*; h, *T. candelabra*; i, *T. macrantha*; k, *T. killipii*; n, *T. floccosa*; o, *T. echiteifolia*; p, *T. boliviana*; q, *T. eriosperma* subsp. *simplex*; r, *T. paniculata*; s, *T. nivea* var. *fasciculata*; z, *T. rytidocarpa*.

De Granville also discussed the forest canopy, which he considered as a refugium for epiphytes such as *Aechmea setigera* Mart. and *Topobea parasitica* Aubl.

Forero (1976) revised the American species of *Rourea* (Connaraceae) and provided clear distribution maps of all species. This paper is cited by Simpson and Haffer (1978), but it does not discuss the distribution of *Rourea* in terms of refuge theory. The distributions are related to the phytogeographic regions of Ducke and Black (1953) and show that the lowland forest of Amazonia is varied and the phytogeographic subdivisions are confirmed by *Rourea*. *Rourea* has many riverine species of inundated forest which are not good examples for the discussion of refugia. However, a few local species fall exactly into refugia areas: *R. ligulata* Baker in the Belém refugium; *R. duckei* Huber in the Guiana refugium; *R. cuspidata* Benth. ex Baker var. *densiflora* (Steyerm.) Forero in the east Peru refugium; and *R. sprucei* Schellenb. var. *subcoriacea* Forero in the Imerí refugium. Also *Rourea glabra* has an interesting disjunct distribution occurring in

TABLE 2. Correspondence between refugia of Prance (1973) and taxa of *Trigonia*. Species marked with an asterisk are also widespread outside the refugium listed.

Nechi	*T. rugosa* Benth.*, *T. sericea* HBK*
Nechi, Santa Maria	*T. eriosperma* subsp. *membranacea* (A. C. Sm.) Lleras*
Catatumbo	*T. rugosa* Benth.*
Paria & Guiana	*T. nivea* Camb. var. *nivea**
Imataca	*T. bracteata* Lleras, *T. reticulata* Lleras
Guiana	*T. hypoleuca* Griseb., *T. coppenamensis* Stafleu, *T. subcymosa* Benth., *T. candelabra* Lleras, *T. villosa* Aubl. var. *villosa* (plus 3 non-edemic taxa)
Napo	*T. macrantha* Warm., *T. prancei* Lleras (plus 2 non-endemic species)
Manaus	*T. nivea* var. *pubescens* (Camb.) Lleras, *T. spruceana* Benth. ex Warm.*
E. Peru	*T. killippi* Macbride
E. coast Brazil forests	*T. rotundifolia* Lleras, *T. rytidocarpa* Casar., *T. paniculata* Warm.

Central America, Colombia, Venezuela, and Roraima, Brazil and disjunct in eastern Brazil in the vicinity of Rio de Janeiro.

Lleras (1978), in a monograph of the Trigoniaceae, treated the refuge theory in some detail basing his discussion on the refugia of Haffer (1969) and Prance (1973). He suggested that the distribution of Trigoniaceae offers further support to the refuge theory since the centers of distribution coincide with those of the four families studied by Prance (1973). The Trigoniaceae has two distribution centers: southeastern Brazil around Rio de Janeiro, Venezuela, the Guianas, and northern Amazonia. The northern group has been most strongly affected by isolation into refugia. Table 2 shows the correspondence between the refugia of Prance (1973) and taxa of *Trigonia*. Fourteen of the total thirty taxa recognized by Lleras correspond well to refugia (Fig. 8) and another six more widespread taxa have their distribution centered on refuge areas, showing that the distribution of the genus does indeed coincide well with postulated refugia.

In addition to the above species of *Trigonia*, which correspond to refugia, Lleras drew attention to the species *T. boliviana* Warm., *T. floccosa* Rusby, and *T. echitifolia* Rusby, which are all endemic to the eastern limit of the Andes in Bolivia. He also commented that with further paleobotanical work in the Amazon basin, a somewhat different distribution of refugia may have to be postulated; these aspects are discussed further below.

One of the most detailed botanical studies of the refuge theory was done in Mexico and Central America by Toledo (1976, 1981). In Mexico there are many more evidences of Pleistocene climatic changes, which are summed up in considerable detail by Toledo. Graham (1981) provided much palynological evidence for the climatic changes in Mexico. Toledo (1976) pinpointed five refugia for Mexico and northern Central America. These were based mainly on evidence from centers of endemism and the distribution of endemic species in a similar way to methods used in Amazonia. Toledo also pointed to other botanical evidences in Mexico:

1. The distribution of temperate elements in areas of tropical rain forests, for example *Quercus* and *Pinus*.

2. The distribution of xerophytic elements in tropical rain forest areas (also one of the evidences discussed by Simpson, 1972).

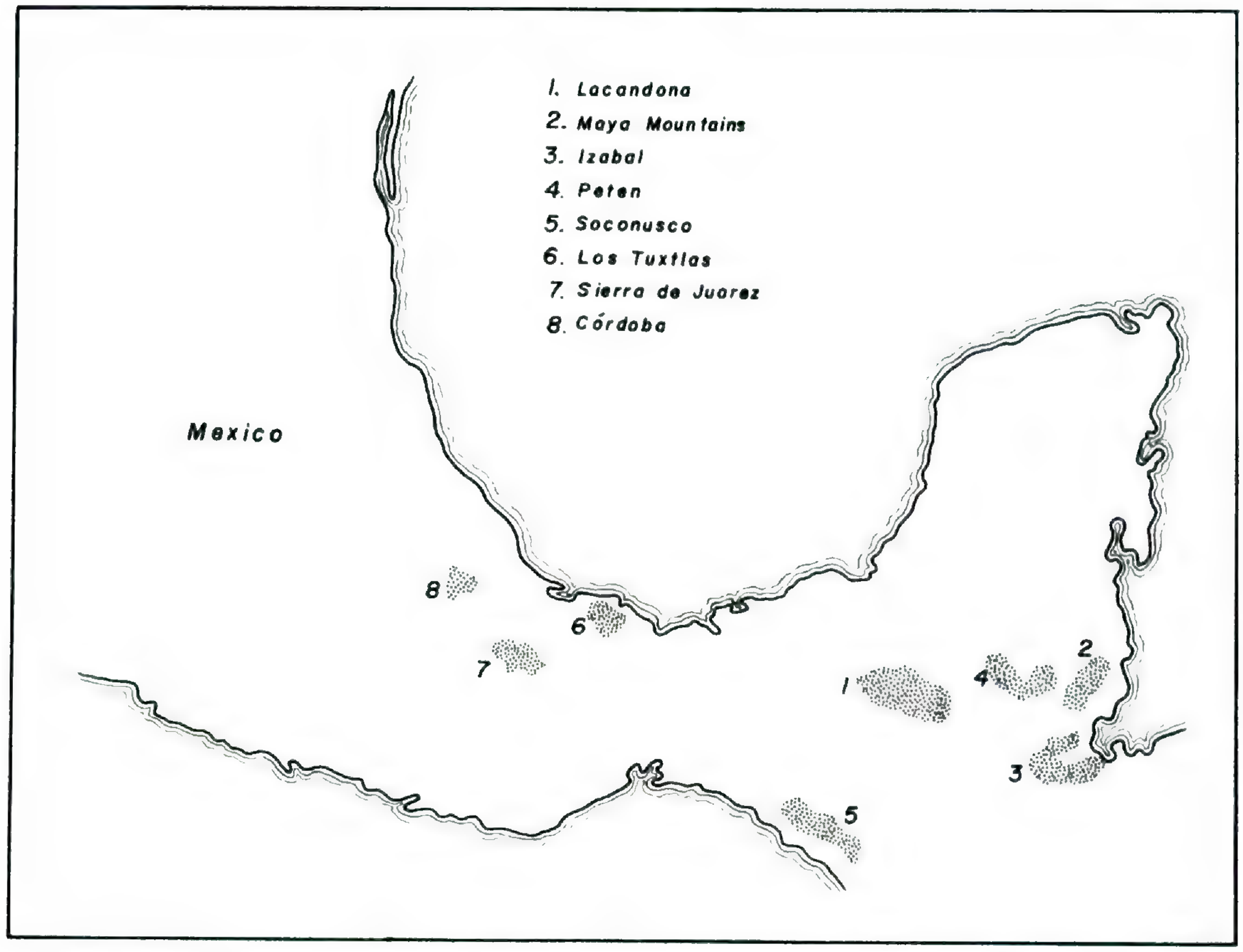

FIGURE 9. The proposed forest refugia in Mexico and adjacent Central America of Toledo (1981). Areas 1–5 are the primary refugia which were also discussed in Toledo (1976) and areas 6–8 are the secondary refugia.

3. The strong tolerance of drought of certain species of the tropical rain forest.

4. Distribution of tropical rain forest species into the cooler climate zones of today. Many examples of this are given, such as *Guarea chichon* C. DC. (Meliaceae).

5. The unusual and differing distribution patterns of the dominant species of the tropical rain forests showing the recolonization capacities of different trees.

6. The latitudinal distribution of tree species.

7. The study of leaf shape and morphology, using the ratio of different types of leaf margin, etc., as an indicator of climate type.

Toledo proposed five refugia for rain forest species during the Pleistocene in Mexico and adjacent Central America (Fig. 9).

1. The Lacandona Region of Chiapas, Mexico.

2. The southeastern portion of Belize in Toledo district including Sierra Maya.

3. Northwest of Sierra Maya around Tikal and Flores in Peten, Guatemala and a part of Cayo District in Belize.

4. The surroundings of Lake Izabal, Izabal Department, Guatemala.

5. The region of Socunusco, Chiapas, Mexico.

The designation of refugia by Toledo is a thorough study with methods which could be applied to Amazonia. The refugia of Central America could have been

important when the recoalescence of the forest occurred because this provided a route for northern species into the northern part of South America. There are some species of Central America with disjunctions well into South America, such as *Licania arborea* Seem. (Chrysobalanaceae), a species common in Central America and the extreme north of Colombia which is disjunct into Amazonian Peru. This type of distribution pattern can probably be explained by the Pleistocene history of the region.

Toledo (1981) discussed further the Mexican and Central American refugia. He gave details of the five refugia defined previously and termed them primary refugia. These areas have the most evidence that they in fact remained as intact units of forest during the arid phases. In his 1981 paper he mentioned three further areas that, because of their high rainfall (over 3,500 mm present day), could also have been refugia for rain forest species. These secondary refuge areas (Fig. 9) were:

1. Sierra de los Tuxtlas in Veracruz.
2. Sierra de Juárez in Oaxaca.
3. The lower slopes of the Sierra Madre in the region of Córdoba in Veracruz.

Further botanical work is needed to determine the role of these areas. The region of Tuxtlas, for example, has endemic species of *Inga, Erythrina, Pithecellobium, Sophora, Ficus, Tillandsia, Heliconia, Olmeca,* etc., as well as subspecific taxa of various plants which would indicate recent isolation.

Gentry (1978) in a general paper about the floristics of Pacific Tropical America, discussed briefly the richness and importance of the Chocó refugium as a source of material for the species rich forest of Panama. His work has shown that the tropical moist forest of Panama is by far the most species rich area in Central America, and its historical relationship to the Chocó refugium is important.

Gentry (1979) discussed refugia in much more detail in relation to the distribution of neotropical Bignoniaceae. He observed that some species of Bignoniaceae fit well into the refugia patterns of Haffer (1969), Prance (1973), and Brown (1976), and also into the phytogeographic regions proposed by Prance (1977) with a slight modification of the western region. While some do fit into the presently accepted pattern of refugia, Gentry observed that many others do not, and also that the collecting sample is extremely poor. He cited, in a table, 19 species of Amazonian Bignoniaceae which were presumed to be local endemics and which have since been collected in far distant places, for example *Tabebuia incana* Gentry first known from Manaus, Brazil, which was collected for the second time on the Río Ucayali in Peru. Such collections show that some species previously considered as local endemics (and used as such for studies of refugia) are in fact widespread. Gentry called the Manaus refugium of Prance (1973) 'controversial' since it was not recognized by many zoogeographers and since 10 species of Bignoniaceae thought to be Manaus endemics have been collected later outside that region. Gentry, however, points out the importance of the consideration of dispersal mechanism of any plant under study and that wind dispersed canopy lianas are perhaps too easily dispersed to have retained present day distribution patterns which can be correlated with refugia. He also provided a good example of the contrasting distribution patterns of the light seed wind dispersal

and heavy fruited mammal dispersed Bignoniaceae which confirm that present day distribution patterns are quite different in the two dispersal groups.

An interesting aspect of Gentry's paper is a discussion of dry forest vegetation species of Bignoniaceae as examples of species in present day 'reverse refugia.' Dry forest areas have contracted today leaving isolated patches which act as contemporary refugia for a different group of species which includes many species of Bignoniaceae, a family well adapted to drier areas throughout its range. Gentry suggested that dry forest Bignoniaceae do seem to provide evidence for the existence of 'reverse refugia.' Many species of Bignoniaceae are restricted to dry forest scattered around the fringes of Amazonia especially in the Interandean valleys of Colombia and Peru and in Central America. Some species, for example *Tabebuia impetiginosa* (Mart. ex DC.) Standl., show little differentiation between their various isolated populations, but others like *T. ochracea* (Cham.) Standl., which has been divided into various taxonomic subspecies by Gentry, appear to be actively differentiating at present. These subspecies correspond to the different contemporary dry forest refugia. Gentry cited further examples of variability in dry forest species and observed that further study of these and similar dry forest disjuncts from other families, from the aspect of refugia should prove useful in the investigation of evolutionary mechanisms in tropical plants.

Gentry (1981) furnished further details about the northwestern part of South America basing his conclusions on his own work in Bignoniaceae and that of Sota (1972) and Lellinger (1975) on pteridophytes. He concluded from his study of the plant diversity of Chocó that there is an unusually high species diversity with a strikingly high rate of endemism (20% of the species studied) concentrated in two or possibly three centers. The closest generic relationship of the flora is with that of Amazonia indicating an Amazonian origin of the flora, but the closest species relationship is with Central America. Many Amazonian families and genera have one or a few outlier species in Chocó, for example Caryocaraceae, Trigoniaceae, *Cariniana* (Lecythidaceae), *Qualea* (Vochysiaceae). Gentry listed 19 examples of species pairs in a table. Gentry concluded that botanical evidence is consistent with the persistence of one or more refugia in Chocó during the Pleistocene dry periods. The endemics of the region fall readily into a northern and a southern group divided near the southern boundary of the department of Chocó in Colombia which indicates a separation into at least two separate refugia.

Another interesting and original part of Gentry's paper is that of evidence from the mangrove flora. The Pacific mangrove flora is markedly richer in species than the Caribbean-Atlantic side. There are six more species in the Pacific mangrove which were confined to the moist areas and restricted in range during the Pleistocene. The fossil record shows a wider distribution of some, for example *Pelliciera rhizophorae* Pl. & Tr., which later became restricted to the Chocó region.

Gentry also presented more evidence about 'reverse' contemporary savanna refugia by discussion of differentiation and subspeciation in *Tabebuia ochracea* (Cham.) Standl. and populational differentiation in species of *Tecoma*. Present day isolation of these species in savannas has allowed differentiation to begin.

Steyermark (1979) presented an extremely detailed account of refugia and dispersal centers in Venezuela. This is the most detailed account of any small

area of South America from the point of view of plant species endemism. In common with many of the other authors already cited, Steyermark began by pointing out the limitations of the present day collection sample for the pinpointing of dispersal centers. He considered the sample in Venezuela as very inadequate even though it is one of the better collected areas of tropical America. Steyermark estimated that the Venezuelan flora consists of between 15,000 and 20,000 species of vascular plants. He outlined well the need to consider the present day geology, physiography, and climate together with the climatic changes of the past. He regards the geological formations and present day physiography as a primary factor in present day plant distribution and endemism, and the historical climate changes as a secondary, but, nevertheless, important factor.

Steyermark differentiated between highland and lowland refugia and pointed out that the highland refugia are associated with mountains, were selected on the basis of the unique floras of various mountains and are not necessarily associated with the climate changes of the recent past. The lowland areas of refugia are, however, associated with climate changes of the past. The principal areas of plant endemism in Venezuela are: the Andes, the Coastal Cordillera, the Serrania del Interior, the Pantepui area, the Gran Sabana, and the edaphic lowland savannas.

Steyermark (1981) outlined the principal forest refugia which have preserved elements of the lowland tropical flora (Fig. 10). These are found in five regions: 1) the coastal Cordillera, 2) the Sierra de Imataca and Altiplanicie de Nuria, 3) the San Camilo forests of Estado Apure in western Venezuela, 4) the forests of lowland elevations in the Catatumbo region and adjacent areas in the Maracaibo basin, and 5) some lowland areas of Guayana including the major refugium of Pantepui.

1. The coastal Cordillera contains nine separate refugia (see Fig. 10) including one on the island of Margarita. There are many wide disjuncts to the south, southeast, and southwest. The close relationship of these areas with the forest of the south of Venezuela indicates that it must have had previous contact perhaps at the height of the Pleistocene humid period or through gallery forest. Steyermark cited numerous examples of both the endemic species and the isolated disjuncts. Species such as *Froesia venezuelensis* Steyerm. & Bunting, *Qualea pittieri*, *Stephanopodium venezuelanum* Prance are good examples of species of predominantly southern genera which occur in the northern refugia. The area of Steyermark's coastal refugia include Rancho Grande and the Paria refugia of Prance (1973), Brown (1976), and others, and Steyermark has broken this down with a thorough examination of the vegetation.

2. The Andean area in the west of Venezuela contains several refugia and dispersal centers all of which are physiographically associated with the mountain ranges. The largest refugium is that of Catatumbo, southwest of Maracaibo, which also corresponds to the refugium of Haffer and later authors. Steyermark points out that many species of Amazonian distribution reach their northernmost limits in the Catatumbo area, for example, *Faramea capillipes* Muell. Arg. (Rubiaceae).

3. The San Camilo area in the west of Apure was not suggested as a refugium by previous authors, although Brown's Apure refugium includes it. Steyermark listed numerous species of Amazonian affinity in this region such as *Licania latifolia* Benth. (Chrysobalanaceae) and *Dichapetalum latifolium* Baill. (Dicha-

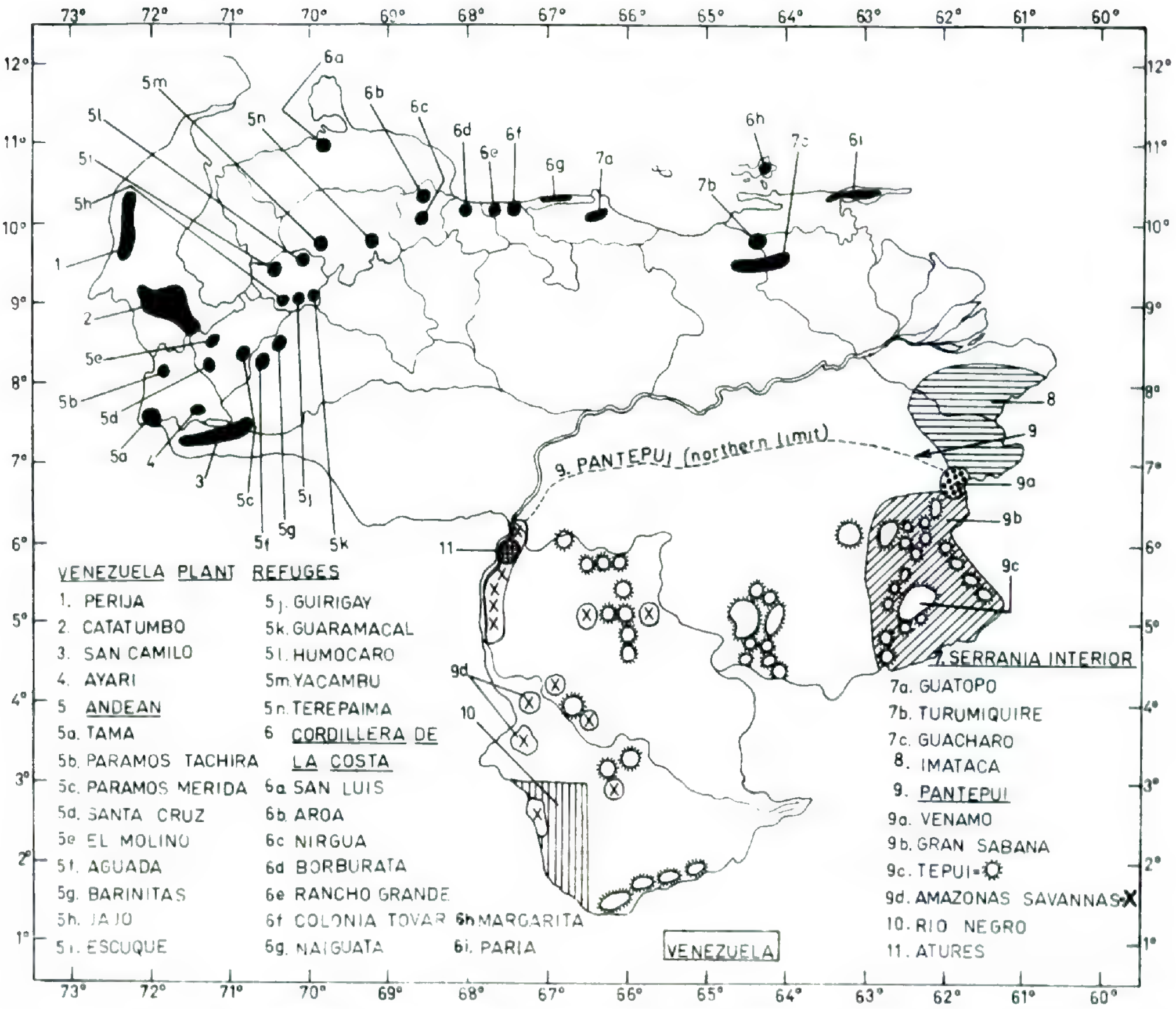

FIGURE 10. The proposed forest refugia (numbered areas) of Steyermark (1981) and location of Tepuis and Amazonas savannas.

petalaceae). *Myrocarpus venezuelensis* Rudd (Fabaceae) also occurs in the San Camilo refugium and is a vicariant species of a genus with the other two species in southern Brazil and Paraguay. Several other small lowland areas around the foothills of the Andes, such as the Ayari refugium in Tachira, are also pinpointed by Steyermark (see Fig. 10).

4. The Imataca refugium is situated just north of Venamo and includes the Altiplanicie de Nuria. This corresponds to the Imataca refugium of Prance (1973), which is extended into Guyana, and also of Brown (1976). The Imataca area has an interesting flora which is intimately associated with the lowland tropical element of the Guianas and Amazonia. Steyermark (1981) furnished a long list of species restricted in Venezuela to the Imataca refugium, as well as a list of endemics such as *Licania latistipula* Prance (Chrysobalanaceae), *Dilkea magnifica* Steyerm. (Passifloraceae), and a list of disjuncts such as *Passiflora spinosa* Mast. otherwise common in western Amazonia.

5. Pantepui as defined in Steyermark (1979) includes the sandstone tops of the Guayana highlands and Gran Sabana in the nearby savanna area. This area includes the Roraima, Ventuari, and Imerí refugia of Brown (1976) and also var-

ious lowland edaphic savannas and igneous lava formations in southern Venezuela. Steyermark stressed the edaphic variability and early history of the region as a cause of much of the endemism that defines his various refugia and dispersal centers in this region. It is interesting that the lowland edaphic savannas of this region have rather a high endemism in contrast to the savannas scattered throughout much of lowland Amazonia. Steyermark pointed out that only 30 genera or 8.5% of the 459 genera are endemic to the summits of the Pantepui, and emphasized the number of summit species which also occur on the slopes. He proposed that distribution from the lowlands to the summits had been much more important than the reverse, which was contrary to the proposals of various previous workers. Within the Pantepui region Steyermark proposed six refugia or dispersal centers:

a. The Guayana highlands refugium with an east-west subdivision.

b. The Gran Sabana dispersal center.

c. The Amazonian savannas of the Río Guainía region such as the Pacimoni savannas and other edaphic savannas on sandy soils.

d. Atures dispersal center, an edaphic center on igneous rock in the Puerto Ayacucho region.

e. The Río Negro, lowland forest refugium. This contains part of the Imerí refugium of other authors.

f. The Venamo dispersal center in the Río Venamo/Cuyari region.

Steyermark's papers are accompanied by large species lists from many different plant families in support of his detailed analysis and conclusions about the Venezuelan vegetation. In this work it is important to differentiate between the endemic centers which are rich because they were refugia, and those areas which are rich as edaphic adaptations to some present day and in many cases also long existent habitat such as the sandstone mountain tops. The number of examples cited makes Steyermark's papers by far the most detailed botanical analysis of endemism and species distribution of any area of South America.

Related to refuge theory and Steyermark's detailed analysis of the Venezuelan vegetation are the studies of Eden (1974) and Huber (1981) of the savanna vegetation of Venezuela. Huber defined three types of savanna in the region: 1) the grassy '*llanos*' type of the north; 2) the grassy inundated savannas of the Manapiare-Parucito basin and, 3) the Amazonian savannas of central and western Venezuela characterized by a high amount of plant endemism or strictly Amazonian floristic elements. These represent centers of diversification of pre-Quaternary origin on sandy soils. The *Llanos* and the inundated savannas, however, are modern relicts of Pleistocene and past Pleistocene climate fluctuations of the hylaea. They show strong floristic relationship of extra-Amazonian savanna types such as the *Llanos*. The important study by Eden (1974) on the paleoclimatic influences on the development of savanna in southern Venezuela treated savannas of the llanos type located along the Orinoco river. Eden proposed that paleoclimatic changes caused the origin of three savannas which he visited. These studies point to the need to distinguish between the different types of savanna in any discussion of the vegetational history of northern South America.

Plowman (1979) considered the biogeography of the genus *Brunfelsia* (Solanaceae) and commented that the complex patterns of distribution of the species

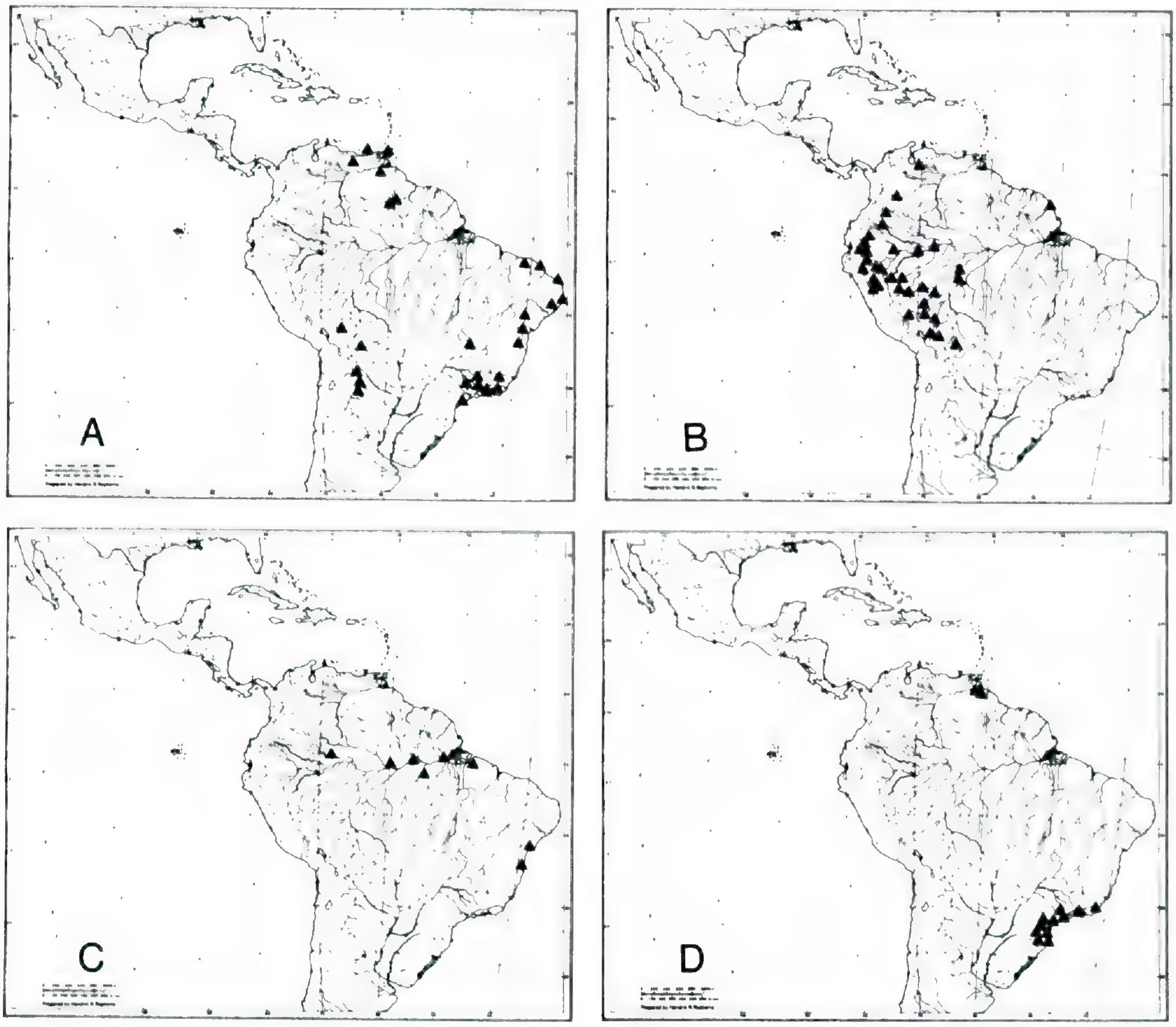

FIGURE 11. Distribution of taxa of *Brunfelsia* (Solanaceae) from Plowman (1979): A, *B. uniflora*; B, *B. grandiflora*; C, *B. martiana*; D, *B. pauciflora*.

of the circum-Amazonian region can only be understood in the context of the past geological and climatic history of South America. A number of taxa of *Brunfelsia* occur in the Amazonian refuge areas, and a number of wide disjunctions occur in the genus. For example, *B. martiana* (Fig. 11) is disjunct between Amazonia and the coastal forests of Bahia, and *B. amazonica* Morton is endemic to the vicinity of Manaus. Plowman concluded, on the basis of the number of local endemics, that the Chocó region has been little changed climatically since before the uplift of the Andes. The most striking Amazonian disjunct is *Brunfelsia grandiflora* D. Don subsp. *schultesii* Plowman, which is widely distributed in the Andean foothills from Venezuela to Bolivia but absent from Central Amazonia and re-occurs in a disjunct population in Amapá, Brazil. The number of endemics in the coastal forest of Brazil as well as the disjuncts with Amazonia and the north, such as *B. pauciflora* (Cham. & Schlecht.) Benth., are evidence of the stability of the Atlantic coastal forests of Brazil. *Brunfelsia pauciflora* (Fig. 11) is common in the Atlantic coastal forests of Brazil and also in the Imatacá refugium in Venezuela. The distribution patterns in *Brunfelsia* correspond well to the forest refugia and Plowman's paper adds further useful botanical evidence of the

influence of the Pleistocene climate changes on the distribution and evolution of plant species. The work of Plowman is interesting because it discusses the isolation of taxa at the sectional, species, and subspecific level.

Northeastern Brazil: Contemporary Refugia

Andrade-Lima (1981) gave a most interesting account of the little known present day forest refugia of the predominantly arid northeastern region of Brazil. Most of the area is covered by the xeric caatinga vegetation. However, forest has persisted on some hills which attract cloud moisture and therefore also have a cooler climate than the surrounding caatinga. These forest patches on hills, termed *brejos* in Brazil, are in a refuge situation. Andrade-Lima listed over twenty such *brejos* which can extend to as low as 500 m (Fig. 12). The species composition of the *brejos* with many Amazonian forest species indicates that they are forest remnants rather than forest formed from easily dispersed colonizers. Such Amazon species as *Manilkara rufula* Miq., *Apeiba tibourbou* Aubl., *Orbignya martiana* B. Rodr., *Parkia platycephala* Benth., and *Virola surinamensis* (Rol.) Warb. are typical of the *brejos*. The *brejos* also contain some forest species of the southern forests of Brazil indicating that they are a most interesting relict with a mixture of isolated species. Southern elements include such species as *Caesalpinia peltophoroides* Benth., *Phyllostyllon brasiliensis* Capanema, and *Myrocarpus fastigiatus* Fr. All. Another species of *Myrocarpus* was mentioned by Steyermark (1981) as a species which has become isolated in the northern coastal cordillera refugia of Venezuela.

Andrade-Lima also mentioned the reverse phenomenon of northeastern arid species which are markedly disjunct having now become isolated by extensive forest or cerrados between their populations. Such species include *Anadenanthera macrocarpa* (Benth.) Brenan, *Amburana cearensis* (Fr. All.) A. C. Smith, *Prosopis ruscifolia* Griseb. and *Schinopsis brasiliensis* Engl.

Multilayered Distribution Patterns

Andersson (1979) discussed the effects of the various contractions and expansions of the rain forest in terms of what he termed 'multilayered distribution patterns.' The effect of the various different climate oscillations are still apparent in present day distribution patterns of *Ischnosiphon* (Maranthaceae) since the effects of the different epochs are found at different taxonomic levels (Fig. 13). Consideration is given to evolution at the sectional, species group, and species level. The patterns of distributions and relationships of each of these levels are discussed by Andersson. Three sections divided into groups of closely related species. The distribution of these species groups are explained in terms of refugia at one time period and that of the individual species within the groups in terms of refugia at a later time. This hypothesis of multilayered refugia has not yet been discussed adequately by botanists. It is certainly supported by the palynological data of van der Hammen (1974, 1981), who has demonstrated clearly the occurrence of many changes in the vegetation of the Andean vegetation. It is also backed up by my own unpublished data on relationships of and within the species groups of the genus *Couepia* (Chrysobalanaceae). The multilayered effect is ob-

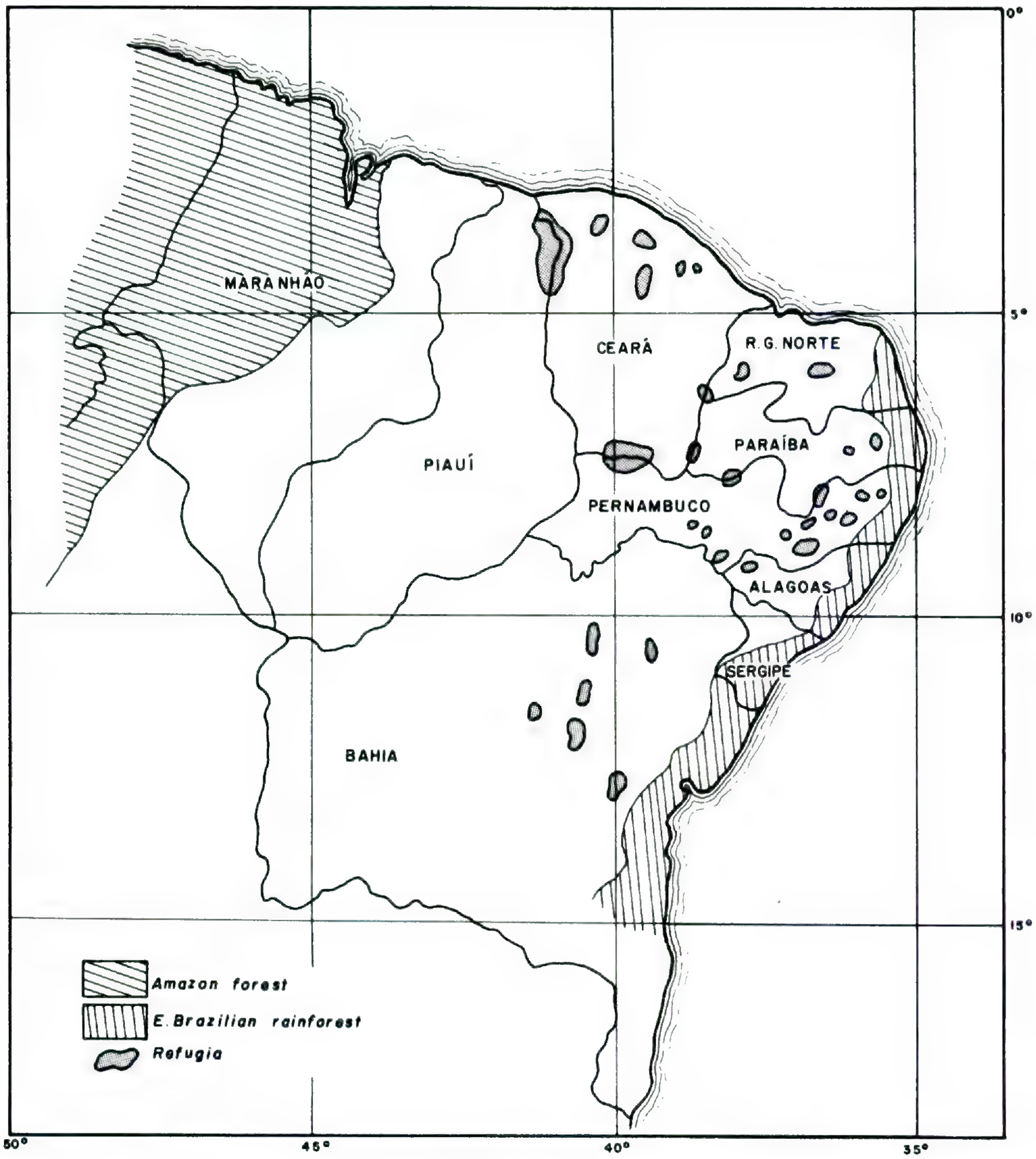

FIGURE 12. Distribution of forest refugia within the predominantly arid northeastern Brazil. Most refugia are *brejos* on low elevation mountains (after Andrade-Lima, 1981).

viously harder to discern and only patterns resulting from the later dry periods are likely to be readily discernible in present day vegetation patterns. This multiple effect of several expansions and contractions of the neotropical vegetation is obviously in need of further study by botanists.

The above review of treatment of the refuge theory by botanists shows that various authors have accepted and commented on the refuge theory, but there are still few detailed studies. Botanical evidences are based on centers of endemism and disjunct distribution and to a lesser extent on xerophytic adaptations of rain forest plants and the variation patterns in polymorphic ochlospecies. The

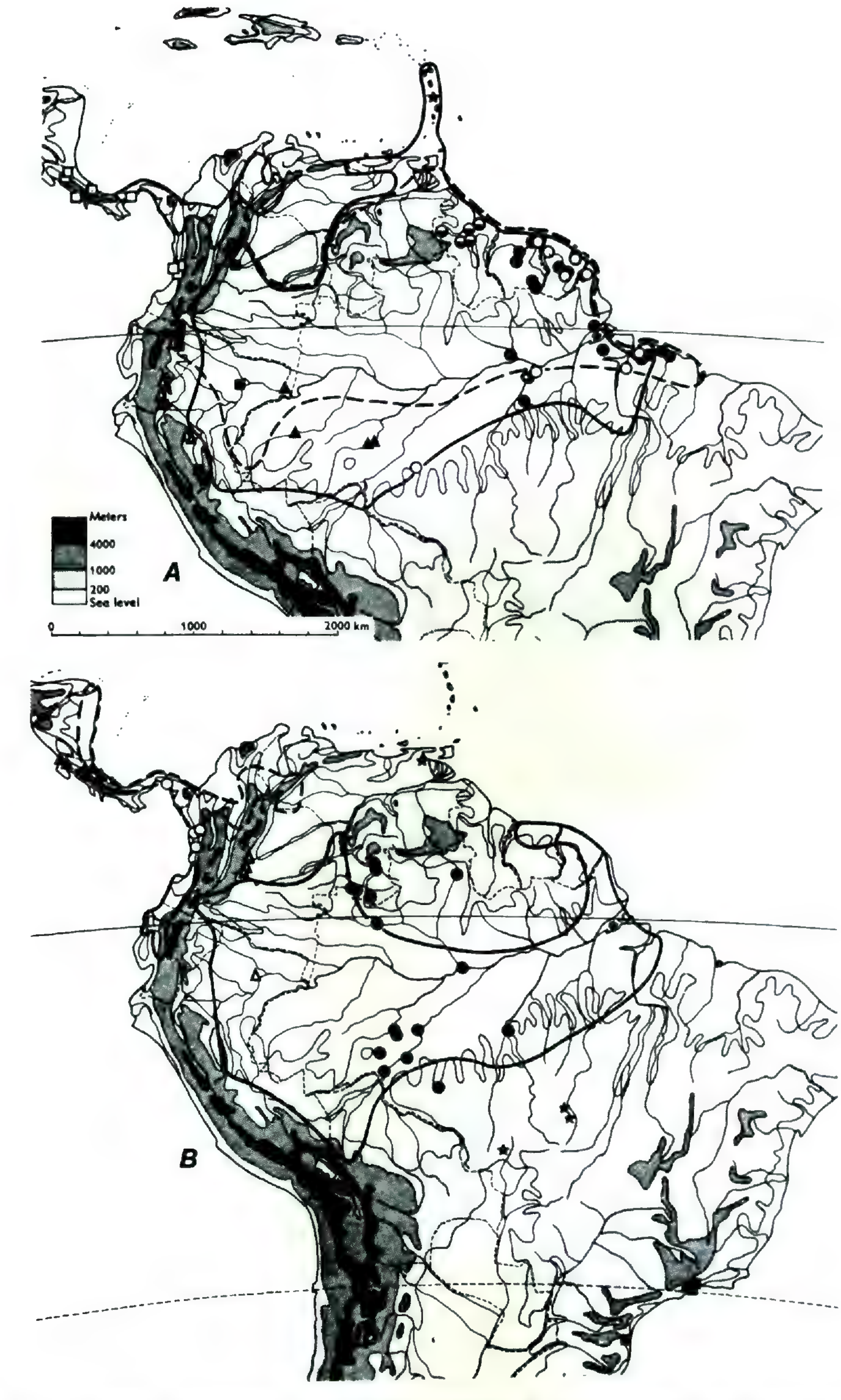

FIGURE 13. The multilayered distribution patterns of *Ischnosiphon* from Andersson (1979).

collection sample is uneven through the lowland neotropics, which also restricts the use of botanical data. However, we now have a good idea of many of the endemism centers. The highland areas are rather different from the lowlands and they offer very definite evidence of the climate changes. Further details of the

highlands are found in B. Simpson (1975, 1978) for the Andean area and in Steyermark (1979) for the Guayana Highlands.

Many of the authors cited have stressed the importance of edaphic adaptations and areas which are endemism centers of significance because of some special habitat. It is important not to confuse these with refugia, for example the white sand vegetation types. Species which are adapted to white sand usually do not occur elsewhere and are often local endemics or disjuncts because of the availability of suitable edaphic conditions. The treatment of Steyermark (1981) for Venezuela gives many examples of these edaphic endemism centers which cannot be regarded as evidence of the effect of historic climate changes on the vegetation.

Several authors cited above have mentioned polymorphic widespread species (ochlospecies in the sense of White, 1962). Examples include *Mouriri grandiflora* A. P. DC., *M. vernicosa* Naud., and *M. guianensis* Aubl. (Morley, 1975); *Licania apetala* (E. Mey.) Fritsch. (Chrysobalanaceae, cited in Prance, 1973) and *Tabebuia ochracea* (Cham.) Standl. (Gentry, 1979). These variable species are not clearly divided into subspecific taxa, yet show considerable morphological variations throughout their range. This can be both in response to present day variables and in response to previous changes. These changes should be studied further in relationship to refugia location and variability.

One of the biggest disadvantages of the methods used for delimitation of refugia in botany is that it is based on the individual taxonomist's concept of species. When centers of endemism and centers of diversity are the only criteria for the selection of refugia, then the individual species are crucial. It is hard to obtain an even species concept amongst taxonomists. This problem should certainly be considered, as evidence for refugia is often compiled based on species distributions. Some of the more sophisticated methods used by zoologists, such as hybridization zones and analysis of variation, are not so dependent upon the individual taxonomist's definition of a species.

The majority of authors cited concur that the refuge theory is likely to apply to their taxa, and have commented on part or all of the forested area of South America. Studying their distribution maps, we have a good idea of endemic centers in the South American tropical rain forest, the most important which are shown in Fig. 4. While the botanical distribution data reflect the well established changes in vegetation cover, their actual role in speciation has been less well defined. A priority for further work is a greater analysis of the speciation which occurred in the isolated refugia.

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CHANGING CENOZOIC BARRIERS AND THE AUSTRALIAN PALEOBOTANICAL RECORD[1]

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ABSTRACT

The first part of this study reconstructs the changing Cenozoic environment of continental drift, tectonics, and climate. The northward movement of Australia brought it into collision with Southeast Asia in Miocene time. Throughout the Cenozoic, New Zealand has remained in approximately the same relative position and the same distance from Australia. Tectonics within Australia have been minor, gentle, and the main topographic features have probably existed in much the same form all through the Cenozoic.

The climate of the early Tertiary was wetter and warmer than that of today, and although the start of desiccation is debated, the present degree of aridity has existed only since the late Pliocene. In the Quaternary, glaciation has been restricted to very small areas in Australia and the glacial periods were more arid than the interglacials. Sea levels have changed throughout the Tertiary as well as the Quaternary. Today, the arid center of the continent is the major feature of the climate. Soils are generally low in fertility, and have been low all through the Cenozoic, when some soils may have been even less fertile than those of today.

In the vegetation today, there are small and disjunct areas of closed forest (= rainforest) in the better watered northern and eastern coastal regions. *Eucalyptus* dominated forests and scrublands cover the major area. Grasslands and shrublands are found in the arid center.

The second half presents the paleobotanical record of all reliable identifications of macro- and micro-fossils, first appearances and the quantitative relationships of the abundant pollen groups. The vegetation must have been closed forest for most of the Tertiary. The nature of these closed forests changes, but open forests only start developing in the Pliocene. The first evidence of grasslands is found in the Miocene of Central Australia, and open savannah and/or grasslands became dominant in southeastern Australia in the Pleistocene. The vegetation was not necessarily more uniform than that seen today, for there is considerable evidence of geographic and time-related variation in the Tertiary floras.

The Quaternary shows cyclic changes of a more open and drier kind of vegetation in glacial periods and a more forested, wetter vegetation in the interglacials.

A comparison of the Australian and New Zealand paleobotanical records shows a general similarity. A number of fossil taxa appear first in Australia and later in New Zealand. The paleoclimate of both has been similar, and distance has not been an insurmountable barrier. The paleobotanical record of Southeast Asia is different, and limited migrations after the Miocene are probably associated with uplift. During the Miocene, there is an increase in Myrtaceae in both Australia and Southeast Asia. It is thought that new availability of soils of low fertility is the cause of this increase in Southeast Asia, whereas both low soil fertility and the developing aridity has been responsible for the increase in Australia.

Climate is the most important environmental factor, for the paleobotanical and paleoclimatic records usually go together. Climate has probably not been a barrier within Australia for most of the Cenozoic, when habitats suitable for closed forest existed in Central Australia, although not necessarily continuous. Some drier areas have probably existed long before the development of the present degree of aridity, allowing adaptations of the flora to develop before these conditions became widespread. Within Australia, tectonics and topography have not been barriers, although they have been important in maintaining habitat diversity. These factors may have been more important as barriers between Australia and Southeast Asia.

This study shows a complex, continuously changing, interwoven environment and flora, rather than migrations stopped or permitted by changing barriers. The concepts of barriers and migrations

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come from historical biogeography, and they seem inappropriate in this study, which essentially follows paleoecological principles.

INTRODUCTION

Areas unfavorable to the growth of plant species constitute barriers to the spread of those species. Fosberg (1963) separates most barriers into the categories of water, topography, climate, and vegetation. Distance may also be regarded as a temporary barrier. Soils, an important factor in Australian phytogeography, may constitute a barrier also. During the Cenozoic, continental drift changes the barriers of water and distance. Tectonic uplift changes topography and climate has been changing continuously. The flora and vegetation have also been changing continuously throughout the Cenozoic. By the beginning of the Cenozoic, the time under consideration in this symposium, the angiosperms had diversified greatly and were a major element in all floras. However, there has been much evolutionary change since the beginning of the Cenozoic, with the appearance of new taxa and extinction of old taxa.

The first part of this paper presents the Cenozoic environment, which is a necessary background to understanding the paleobotanical record. Because a plant taxon requires a suitable environment for growth, its distribution is, for the greater part, controlled by the environment, of which climate is the most important single factor. Some distributions may be adequately explained by a single environmental factor, but frequently a combination of factors produces a more satisfactory explanation. Fossil plants may be used as indicators of past climates. If paleoclimate is reconstructed in such a way and then used to explain past distributions, it would lead to a circular argument. Consequently, the paleoclimate must be reconstructed from independent evidence. Paleobotanical evidence is not admitted here although other biological evidence is admissable. This part of the paper reconstructs the paleogeography, tectonic changes and paleoclimate through the Cenozoic. An attempt is made to reconstruct changes in soil fertility but the evidence available for this is very limited.

In the second part of this paper, the Australian paleobotanical record is presented and possible reasons for changes discussed. The paleobotanical record of New Zealand and Southeast Asia is compared with that of Australia to test the effect of distance as a barrier. Finally, the effectiveness of the barriers discussed above are assessed.

THE CENOZOIC ENVIRONMENT

PALEOGEOGRAPHY

The break-up of Gondwanaland is well known and only movements directly related to Australia and its nearest neighbors are reiterated here.

Separation of Australia from Antarctica commenced at the end of the Paleocene with the formation of a narrow strait, but it was the mid-Oligocene before a deep water channel was formed between the two continents. Australia has moved north some 27° of latitude during the Tertiary (Fig. 1) (McElhinny, 1970; Crook, 1981; Powell et al., 1981).

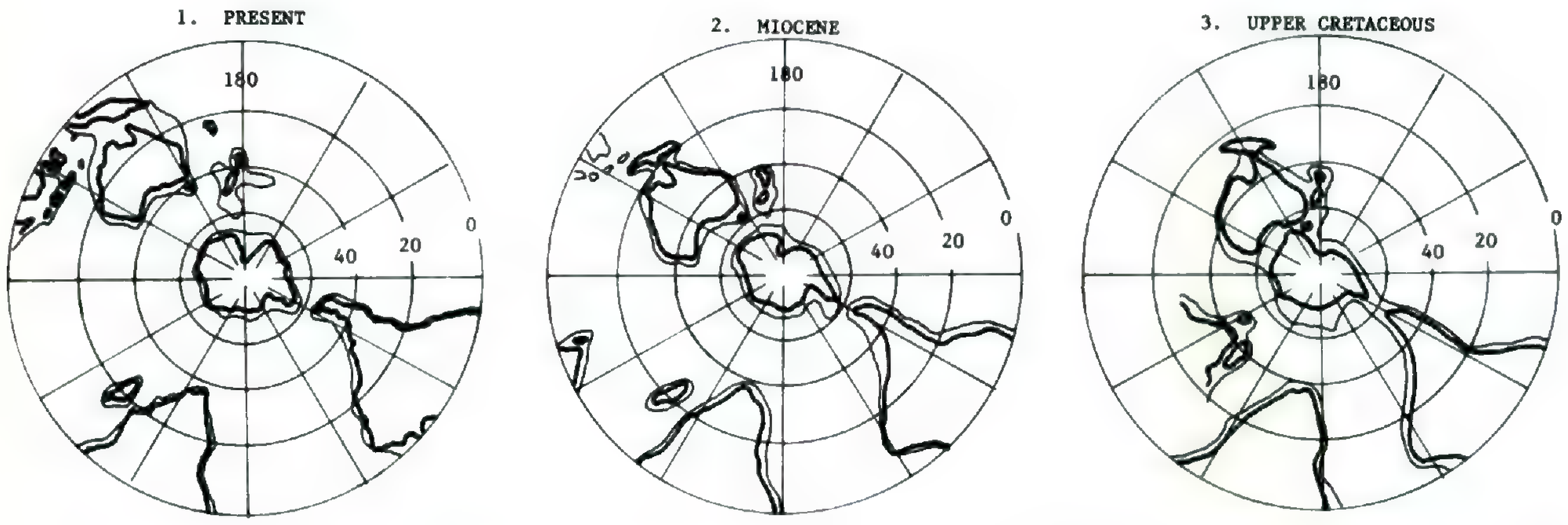

FIGURE 1. Paleogeography showing the relationships of Australia to other continents in the southern hemisphere during the Tertiary. For more detail of the relationships with New Zealand, see Fig. 2 and with Southeast Asia, see Fig. 3.

At the beginning of the late Cretaceous, New Zealand, New Caledonia, and the Lord Howe Rise were closer to each other and to Australia. The opening of the Tasman Sea and the New Caledonian Basin in the late Cretaceous moved these regions further apart. They have remained at approximately the same distance from each other and from Australia for the whole of the Cenozoic (Fig. 2). The distance between Australia and New Zealand is about 2,000 km (Crook & Belbin, 1978; Coleman, 1980; Crook, 1981).

To the north, southern New Guinea has always been part of the Australian plate. The Banda Arcs are very complex and include some fragments from New Guinea. Parts of Timor originate from the Australian continent (Hamilton, 1979). In the early Tertiary, about 3,000 km of deep ocean separated the northern edge of the Australian plate from the southern edge of Southeast Asia. The Australian plate came into collision with the Sunda Arcs of Southeast Asia in Miocene time (15 million years ago). Southeast Asia was probably 2–3,000 km further east and has moved westward, starting about 20 million years ago, but it has always been at the same latitude as the present (Fig. 3) (Powell & Johnson, 1980; Powell et al., 1981).

These movements described above simply present the changing spatial relationships through time, and the latitudinal change of the Australian plate has been the most important (see paleoclimate). Continental drift should not be considered in isolation from other environmental factors that may be more important for biogeography (McGowran, 1979). Climate is the most important environmental factor and there have been global changes throughout the Cenozoic, quite apart from the effect of the changing latitude of Australia. These other environmental factors are presented below.

TECTONICS

Tectonically, the Australian continent has been relatively stable throughout the Cenozoic. Timing of uplift of the Southeastern Highlands is controversial (Bishop & Young, 1980; Wellman, 1980). One school of thought considers that uplift was well advanced by the early Tertiary and was virtually completed by

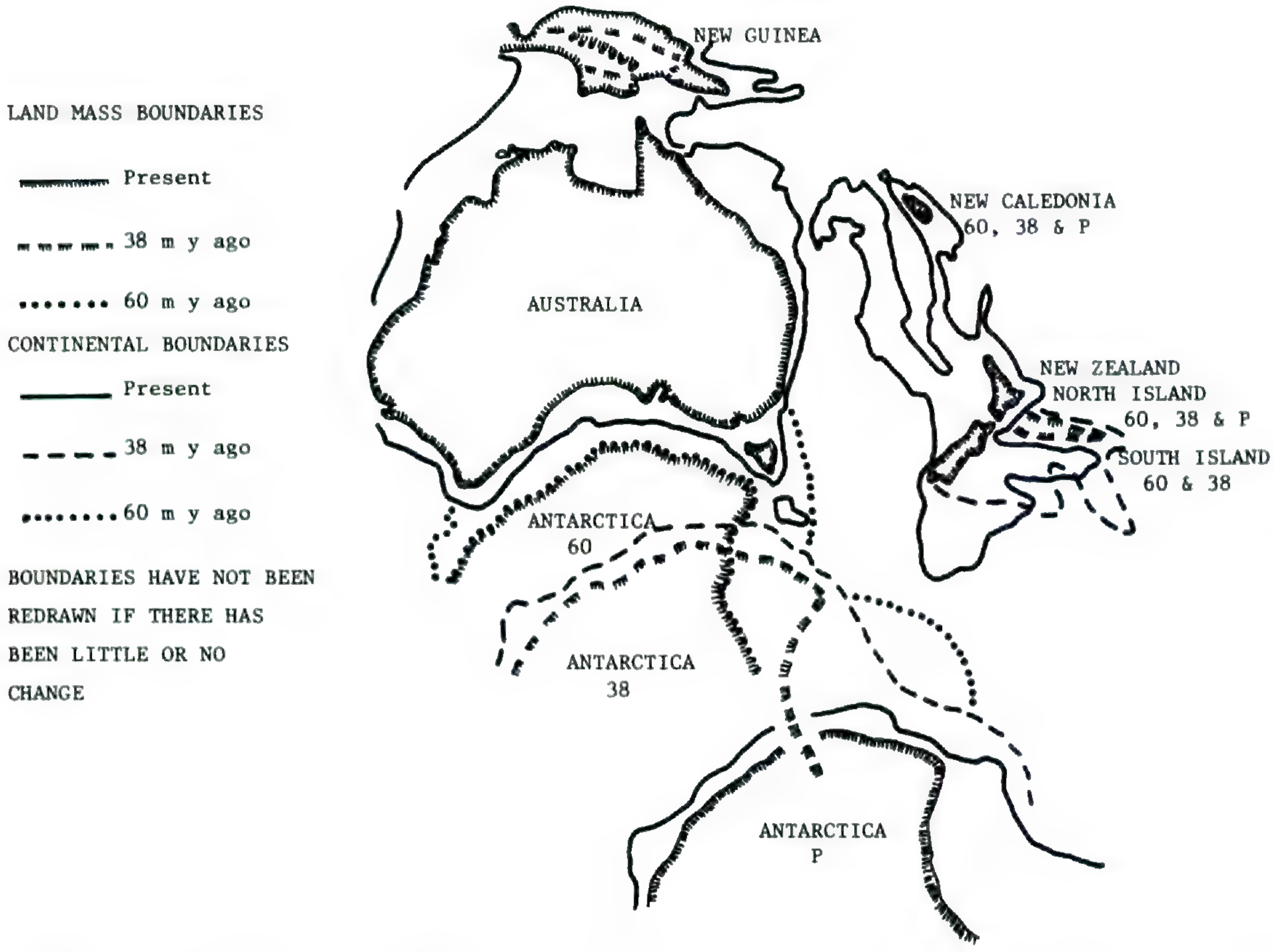

FIGURE 2. Changes in the distance of New Zealand and Antarctica in relation to Australia, constructed from Crook, 1981. Australia is treated as fixed. The boundary of Antarctica for 60 and 38 million years and the present show increasing distance between the two continents. New Zealand has remained at approximately the same distance of 2,000 km from Australia. New Caledonia and New Guinea have remained in approximately the same position, relative to Australia.

Oligocene time (Young, 1977). Another school of thought concludes that uplift has been going on continuously at a steady rate all through the Tertiary (Wellman, 1979). Uplift in the east, in South Australia, and in the west has been going on in stages during this time, and is probably still going on, as indicated by the occasional earthquake. There has been subsidence in central Australia and upwarping of parts of Western Australia. A series of lakes in central Australia was fed by the great internal drainage system. Shallow seas encroached from parts of the western and southern coasts but these marginal basins have been only slightly disturbed. All of these movements have been episodic, relatively small, and moderate (Brown et al., 1968; Ollier, 1977). Relief may have been higher in the early Tertiary (e.g., Young, 1977) but was probably not substantially greater than the present in the late Cenozoic (Galloway & Kemp, 1981). Various lines of evidence suggest that upland areas and drainage patterns of the early to mid-Tertiary were much the same as those of today (Nix, 1981). Australia is a low, flat land mass with most of the relief less than 1,000 m. The highest point, Mt. Kosciusko, is 2,228 m.

PALEOCLIMATE

Continental movement has had a major effect on climate through the initiation of the circumpolar current. With Australia and South America attached to Ant-

FIGURE 3. The position of Australia in relation to Southeast Asia. The position of the Australian and Indian Plates for present and 10, 20, 30, and 60 million years ago are shown. In the early Tertiary there was 3,000 km of deep ocean between the Australian and Southeast Asian Plates. The two came into contact 15 million years ago, in the Miocene. Modified from Powell and Johnson, 1980.

arctica, this current could not operate and the warm equatorial currents travelled to higher latitudes along the eastern margins of the southern continents, effecting a greater heat transfer from the low to the high latitudes. Once the circumpolar current came into operation, it effectively blocked the equatorial currents from travelling into the higher latitudes, thus limiting the heat transfer to these regions.

During the initial drift of Australia away from Antarctica the seas between the two land masses were shallow and the circum-Antarctic current was blocked by the South Tasman Rise, which linked Tasmania to Antarctica. To the end of the Eocene, the Southern Ocean was relatively warm and Antarctica largely nonglaciated. In the early Oligocene, substantial sea ice began to form and widespread glaciation developed on Antarctica. The clearing of the South Tasman Rise about mid-Oligocene time and the opening of Drake Passage between South America and Antarctica about the Oligocene-Miocene boundary (Barker & Burrell, 1977) allowed complete circumpolar circulation. The Antarctic ice cap formed about mid-Miocene time. The volume of ice has increased since this time and was greater than that of the present in the late Miocene (Kennett, 1977; Kemp,

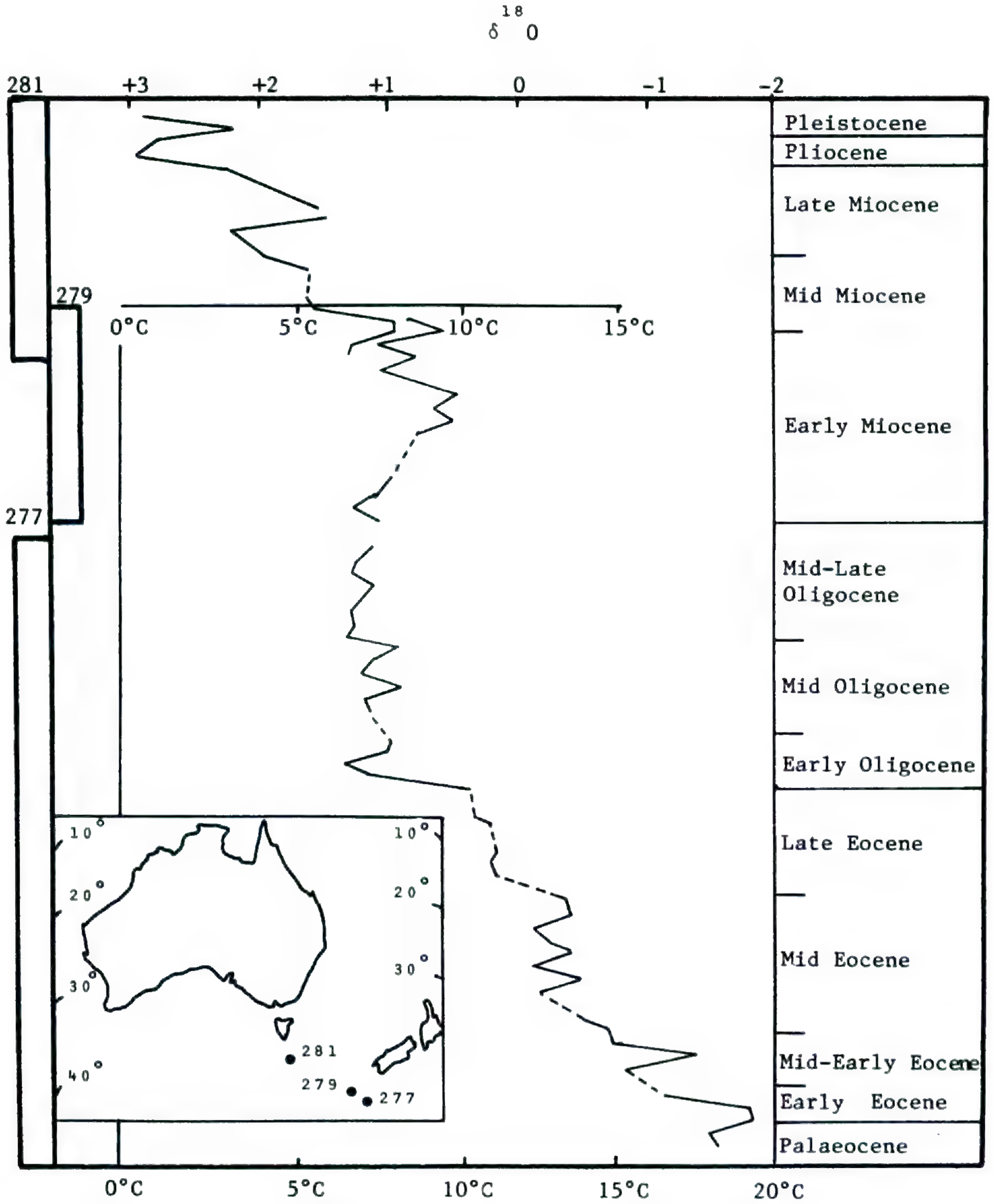

FIGURE 4. Oxygen isotope paleotemperatures, modified from Shackleton and Kennett, 1975. $\delta^{18}O$ is the correction for the change of the ratio of the isotopes in sea water through the Cenozoic. Note: Sites 277 and 279 on the Campbell Plateau were about 50°S in the early Tertiary. The composite curve presented here represents the paleotemperatures of latitudes 40–50°S, for the whole of the Cenozoic.

1978, 1981). The decline in temperature during the Cenozoic is shown by the oxygen isotope temperature curve from deep sea cores on the Tasman Rise and Campbell Plateau, which have remained at latitudes of 40–50°S for the whole of the Tertiary (Fig. 4). There was an overall decline through the Eocene and substantial drops in temperature during the early Oligocene and after the mid-Mio-

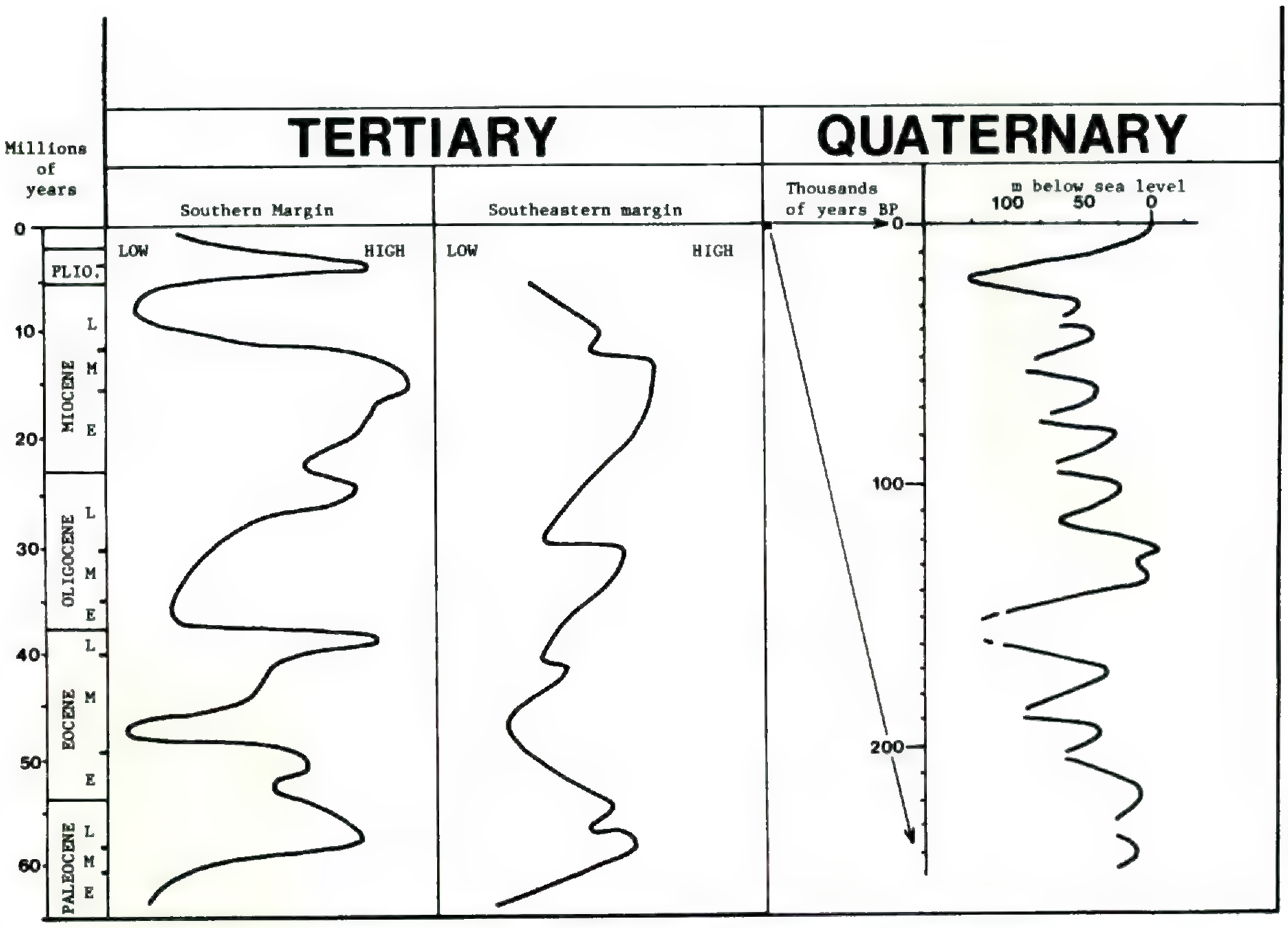

FIGURE 5. Cenozoic changes in sea level in the Australian region, from the sedimentary cycles of Loutit and Kennett, 1981, and Chappell, 1978. The two Tertiary curves show sedimentary cycles on the continental margins and changes in sea level have been the major factor determining deposition. There is an overall agreement but they are not identical because of slightly different histories of deposition. The Quaternary curve for sea levels is for the last 250,000 years only. For further explanation, see text.

cene (Shackleton & Kennett, 1975). Throughout the overall decline, there are many fluctuations. That these fluctuations are important, biogeographically, is shown by the foraminiferal record. Tropical foraminifera show a number of short-lived excursions into the higher latitudes, and these excursions show a good fit, on the whole, with the oxygen isotope curve (McGowran, 1978).

Changes in sea levels through the Cenozoic have alternately exposed and drowned the continental shelves. Figure 5 shows two Tertiary sea level curves taken from Australian sedimentary cycles. A third, from the Western Australian continental shelf (Quilty, 1980), is very similar to the southern Australian curve shown on Fig. 5. The two curves show an overall agreement, but are not identical because of the different histories of deposition (Loutit & Kennett, 1981). These cycles in sea levels can be equated, in a general way, with world wide changes (Vail et al., 1977). It is thought that geotectonics, variations in rates, and directions of sea floor spreading, etc., have been the cause of these changes. The eustatic glacial cycles of the Quaternary are superimposed on the longer term cycles, although there was some glacial influence on sea levels before the Quaternary. At times of high sea levels, shallow flooding of the continental shelves and low lying areas results in a warm, wet climate. At times of low sea level, the low lying areas are drained and the continental shelves exposed, resulting in a climate that is cooler and drier.

The long term changes in sea level through the Cenozoic are measured in

terms of millions of years while the glacial cycles of the Quaternary can be expressed in terms of thousands of years. Figure 5 shows the sea level changes over the last 250,000 years (Chappell, 1978). This curve has been constructed from coral reefs in New Guinea, Timor, and the Barbados and shows a number of fluctuations between the major interglacial high levels.

Oceanic circulation and the development of the ice cap on Antarctica has had a major influence on Australian paleoclimate. Kemp (1978, 1981) used data from deep sea sediments to model atmospheric circulation. There are, however, many indications on the land itself as to the nature of the paleoclimate, although much of it is not as reliably dated as that of the deep sea cores. There is abundant evidence that inland Australia was once much wetter than today. Residual laterite and kaolinized profiles are widespread in Australia, including the arid region. The chemical weathering required to produce these profiles would require a warm, humid climate with a much higher rainfall than that received in inland Australia today. The ages assigned to laterite in the various regions are different, because there has been more than one episode of lateritization (Hayes, 1967; Alley, 1977; Idnurm & Senior, 1978). Paleomagnetic dating suggests that the dominant period of lateritic weathering over a large area of Australia was late Oligocene to early Miocene (Schmidt et al., 1976). The Cenozoic stratigraphy of the Lake Eyre Basin indicates an alternation of relatively humid and dry periods, but the present degree of aridity did not appear until the Quaternary (Jessup & Norris, 1971). In the Lake Frome area, the climate of the Miocene was subtropical or warm temperate with a relatively high rainfall and, at times, seasonal dry periods became a part of the weather pattern. Arid and pluvial climates alternated in the late Tertiary and Quaternary (Callen & Tedford, 1976). River systems in the arid region of Western Australia have been inactive since middle Miocene time and are now reduced to a chain of salt lakes (van der Graaff et al., 1977).

The aridity of the Australian continent reached its present proportions in late Pliocene-Pleistocene time, about 2.5 million years ago (Bowler, 1976). There is some debate as to how the present state of aridity was reached. One school of thought places the first beginnings of a drier climate in the Eocene, using the notion that offshore terrigenous sediments infer river drainage (Quilty, 1974) and that the change from terrigenous to carbonate sedimentation is an indication of the cessation of efficient drainage from the land. (This hypothesis contradicts the paleomagnetic dating of laterites, discussed above, if the possibility of fluctuations in climate is ignored.) Another school of thought interprets the same evidence as indicating drainage from a flat, well-vegetated terrain with a consequent lack of erosion. This second school of thought places the start of desiccation in the late Miocene (Bowler, 1976). There is general agreement, however, that at least localized dry areas have probably existed in inland Australia long before the present state of aridity was reached. If, during the Tertiary, very small pockets of aridity existed amid large areas of better watered country, they may be very difficult to detect by normal geological and paleontological methods. Such small pockets would be biologically very important, for they would allow the evolution of a genetic complement suited to the arid environment, forming a nucleus for later expansion.

The climatic changes of the Tertiary are described in terms of million of years, but those of the Quaternary may be described in terms of thousands of years. Bowler et al. (1976) have reviewed evidence of the climates of the last 60,000 years. From 25,000 to 15,000 years B.P., which includes the last glacial period, it is estimated that the mean annual temperature was lowered by 6–10°C. Glaciation was restricted to Tasmania and small areas in the Snowy Mountains, although periglacial activity extended much further in the Eastern Highlands. There is considerable evidence of a drier climate throughout the whole time, although in southern Australia lakes filled at the time that temperatures were lowest, probably as a result of reduced evaporation. In the last 10,000 years, the climate has been relatively stable.

Nix and Kalma (1972) have constructed models of changes that have occurred since the last glaciation. These models (see Fig. 6) include the postulated type of vegetation that would result from the climate prevailing at the time, but they have been built from the climatic controls of the vegetation. These models reflect the major influence of lowered sea levels that accompanied maximum glaciation. With the sea level at the margin of the continental shelf, the continentality of a low land mass such as Australia would be increased considerably. With deeper, colder seas surrounding Australia, evaporation and hence precipitation would be less. Changes similar to these must have happened many times during the Quaternary as the sea level oscillated with the glacials (see Fig. 5). Evidence from soils (Butler, 1967) and hydrologic regimen (Schumm, 1968) indicate alternating phases of unstable erosion/deposition and stable non-erosion/non-deposition during the Quaternary. It is thought that the disturbing effect of an unfavorable climate reduces the vegetation cover and erosion is accelerated. Such cycles of instability and stability of only a few thousand years duration must have had a profound effect on the biota.

THE CLIMATE TODAY

Aridity is the major feature of the climate of the Australian continent today. More than two thirds of the continent receives a mean annual precipitation of less than 500 mm and a third has values of less than 250 mm. Precipitation zonation is roughly concentric with the highest values across the northern edge and down the eastern coastal strip. Even the well-watered coastal regions receive a seasonal precipitation so that 80% of the continent has at least three months of the year without effective precipitation. Roughly the northern half of the continent receives summer precipitation and the southern half winter precipitation. New Guinea and Western Tasmania are the only significant areas of a humid climate receiving more than 2,000 mm mean annual precipitation.

For biogeographic purposes, the extremes of temperature are perhaps more instructive. All but the highest elevations near the coast of continental Australia receive mean daily maxima exceeding 30°C during the hottest part of the year. In the coldest part of the year, freezing temperatures and frosts occur regularly over roughly half the continent. For a more detailed discussion of the climate, see Nix (1981).

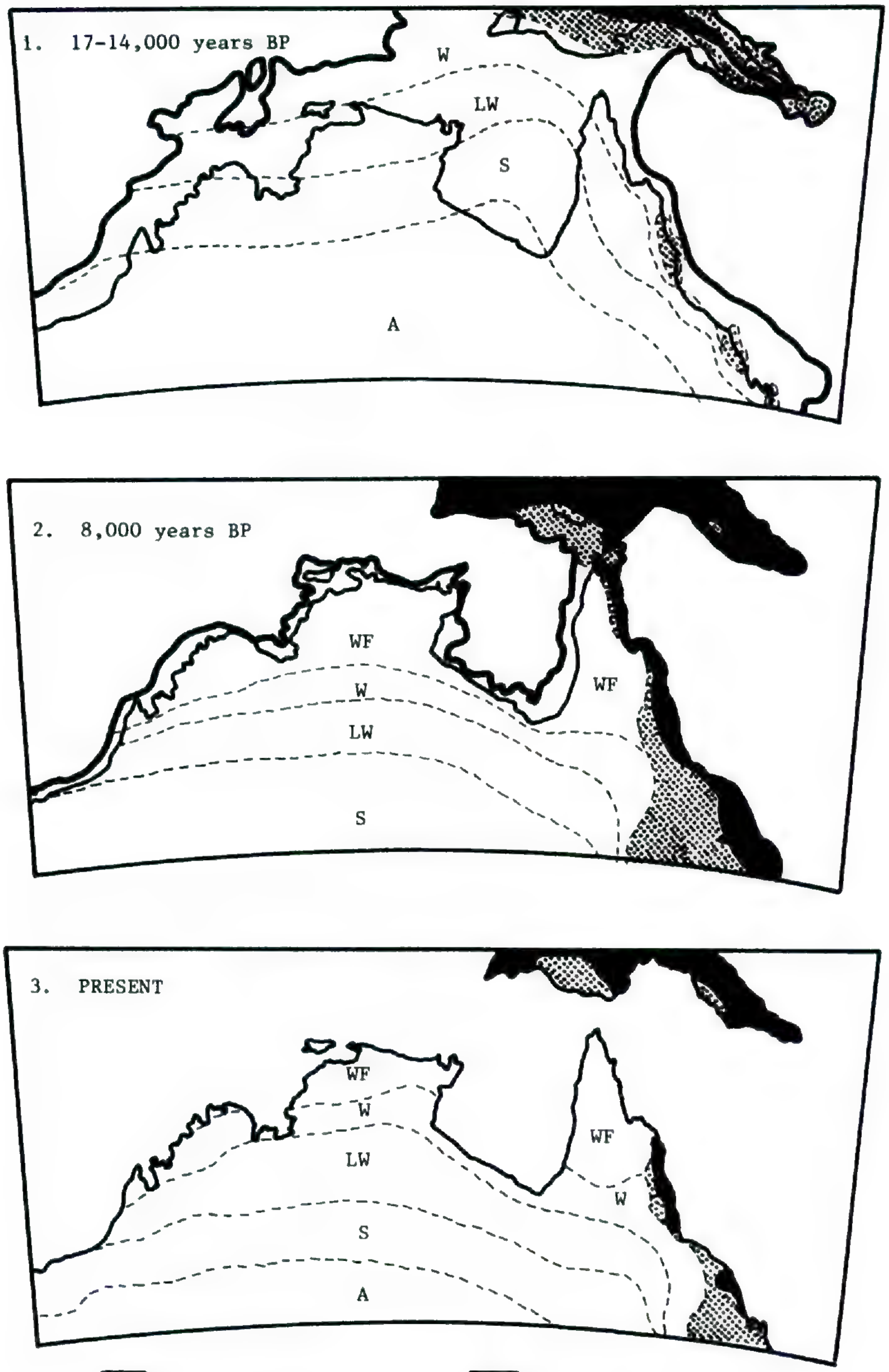

FIGURE 6. The main types of vegetation that might result from the climate postulated for stages since the last glacial period, from Nix and Kalma, 1972. 1. For the period of maximum sea level lowering. The loss of warm shelf water has greatly reduced precipitation and continentality has increased. The arid vegetation would have expanded and the closed forest (= rainforest) contracted, with a corresponding shift of the intermediate types. 2. For the period of rapid rise in sea level and rapid warming of very shallow shelf water, resulting in a greatly increased precipitation. Temperatures are slightly higher than those of today. The closed forest would have expanded considerably and the

SOILS

"There is probably no continent with soils so generally low in key plant nutrients as Australia . . ." (Bowen, 1981). Soils of high and moderately high nutrient status are restricted to an archipelago of islands on the Australian continent although they are fairly extensive in New Guinea. Soils of low and very low status are widespread and probably cover more than half the area of the continent. Gross deficiencies exist in both major and minor nutrient elements (Nix, 1981).

The low nutrient status of the soils is attributed partly to the mainly sedimentary parent material, and mostly to the prolonged deep weathering of the landscape and the stripping and reworking of older soil profiles (Nix, 1981). Since the present low status results from the once wetter climate and resultant processes of lateritization that were in progress during the early Tertiary, then the soils must have had a low nutrient status all through the Cenozoic.

There is some evidence of change in nutrient status of the soils during the Cenozoic. Volcanism has provided restricted areas of new parent material and has produced the islands of higher nutrient soils. In a second example, numerous water bores in western New South Wales have revealed two formations in the Cenozoic alluvium. The older, underlying formation contains sands and gravels that are almost entirely quartz and it is predominantly grey in color. The younger, overlying formation is varicolored, frequently red-yellow-brown and the sands and gravels are an admixture of the various rock types exposed in the catchment today. It is thought that the quartz in the underlying formation came from extensive quartz gravels that once blanketed the region but have now been eroded away except for remnant hill-cappings (Williamson, 1964). However, the transition between the two formations is time transgressive; about mid-Miocene in the western region on the riverine plain and late Pliocene–early Pleistocene in the eastern region in the river valleys. The pollen assemblages of the two formations always indicate a wetter climate for the lower and a drier climate for the upper formation (Martin, 1973, 1977a). This evidence suggests that there is at least a climatic component in the development of the two formations. Although there are no direct measurements, soils formed on predominantly quartz, under a wetter climate, are likely to have had a lower nutrient status than those of today that are formed on a variety of rock types with less weathering. Thus the little evidence available suggests that during the Tertiary, some soils were even less fertile than those of today.

The Vegetation Today

So that past changes in the environment and the vegetation may be fully appreciated, a brief outline of the phytogeography and the factors controlling the

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arid vegetation would be much reduced. 3. Present day, with deeper, cooler shelf water and the cooling effects of the current through Torres Strait. Temperatures and precipitation are slightly lower. There is a slight retreat of closed forest and an expansion of the arid vegetation. W, woodland. LW, low open woodland. WF, woodland/open forest. S, shrubland. A, arid vegetation.

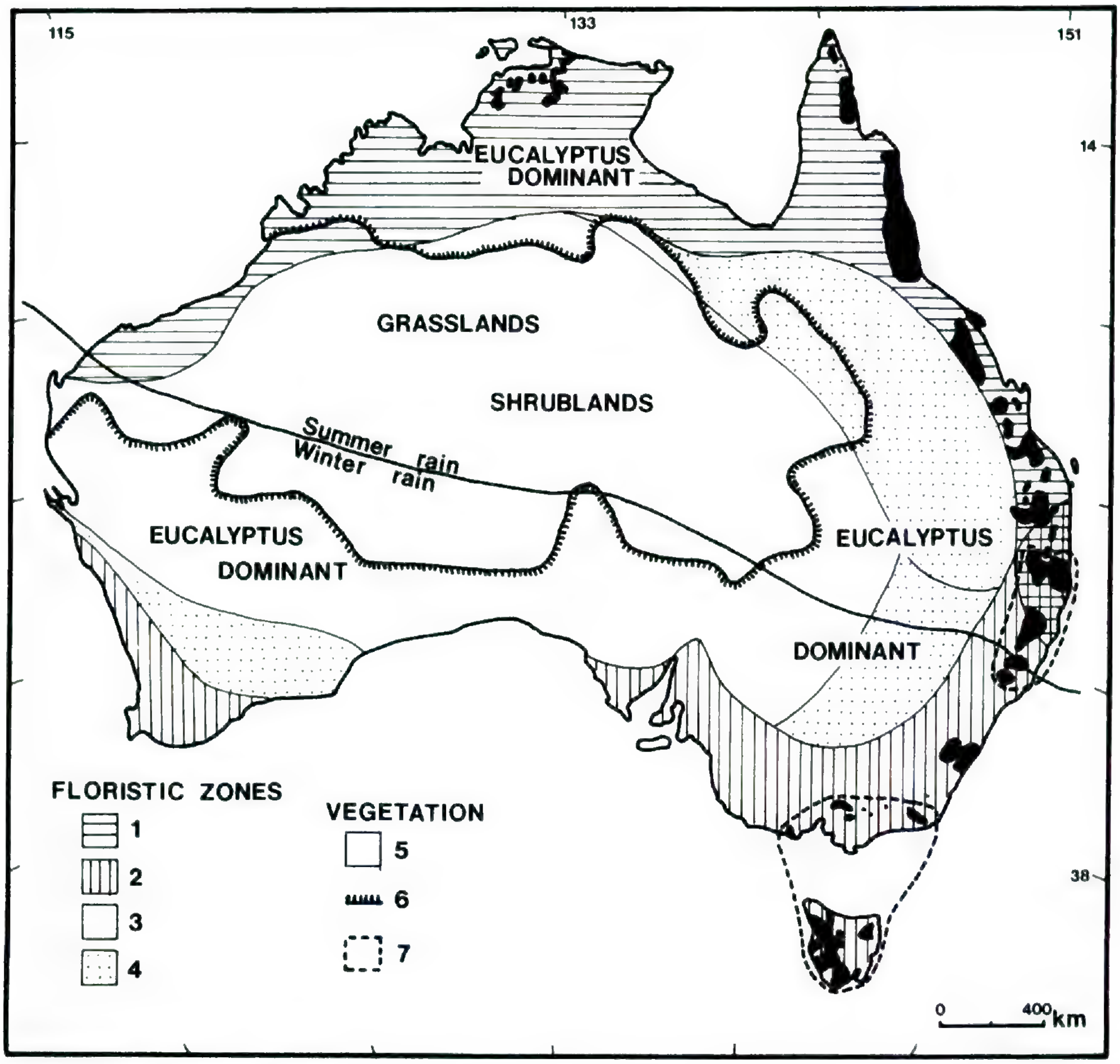

FIGURE 7. The floristic zones (from Burbidge, 1960) and major categories of vegetation (simplified from Specht, 1970 and Webb & Tracey, 1981b). 1. Tropical zone. 2. Temperate zone. 3. Eremaean zone. 4. Interzone areas. 5. Closed forests (= rainforest). 6. The boundary between *Eucalyptus* dominated communities and those with a mixture of dominants. 7. Areas where *Nothofagus* may be found in the closed forests. For further explanation, see text.

vegetation today are presented. Figure 7 shows the three main floristic zones recognized by Burbidge (1960), the discontinuous distribution of rainforest, and the approximate limits of the dominance of *Eucalyptus*. In most of the Eremaean Zone, *Eucalyptus* is present but not dominant. *Acacia* is one of a mixture of dominants here, but it is also very common in the understory where *Eucalyptus* is dominant.

There are small areas of rainforest (= closed forest) along the northern and eastern coast (see Fig. 7). Although the rainforests are located in areas dominated by *Eucalyptus*, the latter is not a normal constituent of mature rainforests and there are few floristic affinities between adjacent rainforest and eucalypt communities. Tree species of mature rainforest must be able to regenerate under a well-developed or only slightly disturbed canopy. The rainforests are monsoonal and tropical in the north, subtropical and warm temperate along the east coast,

and cool temperate in the southern limits of their range. Tall closed forests require about 1,500 mm of precipitation per annum for extensive development (Francis, 1951), although rainforest elements growing as low forest with emergent *Araucaria* may receive only 900 mm p.a. (see Webb, 1978). Small pockets of rainforest may be found outside of the general climatic limits where the available moisture is supplemented, e.g. by seepage, mountain fog, or soils of higher fertility, especially in fire shadows that are protected from wild fires. These pockets may be only a few hectares in area, too small to be mapped, but biologically they are very important. In areas that are climatically favorable, the most complex rainforest is restricted to the soils of higher nutrient status or niches favorable for nutrient accumulation. Provided rainfall is high, soils of lower nutrient status may support simple evergreen types of rainforest that are typically mixed with sclerophylls. *Eucalyptus* and sclerophylls are dominant on the lower nutrient soils, which do not support rainforest especially where exposed to wildfires. *Nothofagus*, which is so conspicuous in the paleobotanical record (discussed below), is restricted to the areas shown on Fig. 7 where it is one of the few taxa of trees in mature temperate rainforest (Webb & Tracey, 1981a, 1981b; Howard, 1981). *Eucalyptus* requires light for germination and, even under a disturbed canopy, usually requires exposure of mineral soil for establishment.

The region dominated by *Eucalyptus* may be divided into (1) tall open forest, (2) open forest, (3) woodland, and (4) scrubs and shrublands. These divisions broadly follow the rainfall gradient with the tall open forests in the wettest and the scrubs and shrublands in the driest regions.

In tall open forests (or wet sclerophyll), the eucalypts are from 40 m to 100 m in height and there is a shrub layer of mesic taxa. In many places, eucalypts are emergent above well-developed rainforest. Such forests are clearly successional and are potentially capable of developing into rainforest. Tall open forests are found in the higher rainfall areas or the more protected sites. Because *Eucalyptus* requires light for germination and rarely regenerates under a closed canopy, fire regenerates and shapes the development of these forests. If fire is too frequent, i.e. before the eucalypts reach flowering age, it will eliminate *Eucalyptus*. Fire also prevents the succession proceeding towards rainforest (Ashton, 1981).

The eucalypts in open forests (or dry sclerophyll) are quite variable in height but less than 30 m. Moisture relationships appear to be the most important factor for tree growth and density. The hard-leaved shrubby layer, so distinctive of the dry sclerophyll forests is found on the more infertile soils, whereas the understory is grassy on soils of a better nutrient status (Gill, 1981). Efficient nutrient cycling is important on the infertile soils. Nitrogen fixation, mycorrhiza, and proteoid roots enhance the mineral status of the sclerophyllous communities (Bowen, 1981). At least one species of *Eucalyptus* utilizes insoluble phosphate (Mullette et al., 1974). Added fertilizers may increase growth of sclerophyllous shrubs, but then the shrubs may also become more drought susceptible (Specht, 1963). The slower growth rate imposed by low soil fertility may confer drought resistance (Parsons, 1968). In general, any means of increased drought resistance involves a cost to the plant in a reduced growth rate (Cowan, 1981). Thus the mechanisms of coping with low nutrient status and water stress may not be independent.

Grassy woodlands (savannah woodlands) characterized by well-spaced trees

are generally found on the better soils. Almost all of the woody taxa belong to either *Eucalyptus* or *Acacia* (Gillison & Walker, 1981).

Scrubs and shrublands (or mallee) are dominated by *Eucalyptus* with many stems arising from an underground lignotuber (mallee growth habit). Some species of *Eucalyptus* may grow both as a tree or a mallee, depending on growing conditions. The dominants are 2 m to 8 m in height. *Acacia* is also common here. The understory consists of sclerophyllous shrubs on the infertile soils, sparse grasses on the more fertile soils and chenopodiaceous shrubs in the drier regions (Parsons, 1981).

Shrublands and grasslands are the major vegetation types in the Eremaean Zone. Species of *Eucalyptus* are present but not usually dominant. Shrublands may have both large and small shrubs. The abundant large shrubs include *Acacia* and, less frequently, the mallee form of *Eucalyptus* (Johnson & Burrows, 1981). Chenopodiaceous shrubs are common in the southern part of this zone (Leigh, 1981). Tussock (*Astrebla*) and hummock (*Triodia* and *Plectrachne*) grasslands are found in the northern part of the arid region (Groves & Williams, 1981). Throughout, the low and erratic rainfall is the controlling factor. Nutrient status is generally low because the soils have been formed on the highly weathered and leached parent material. However, the most important soil characteristics are those that control the amount and availability of water (Perry & Lazarides, 1962).

THE PALEOBOTANICAL RECORD

Reconstructions of the flora and vegetation presented here come mainly from pollen studies. Work is in progress on macrofossils and provides much valuable evidence but it is not yet sufficient to be used for the reconstructions that are possible from pollen. When relying on evidence from pollen, it is important to bear in mind that there is a bias. When pollen and leaves have been identified from the same deposit, the two assemblages may contain quite different taxa. For example, mid-Eocene deposits contain pollen of *Nothofagus* and Myrtaceae but no leaves of these taxa (Christophel, 1981a). The reason for this difference is that leaves are derived mainly from the margins of the site of deposition of clastic sediments so that stream-side taxa are overrepresented. In coals and peats, however, leaves are produced on site. Most leaves do not transport well. On the other hand, pollen in a sediment is derived from a much greater area, probably the whole of the catchment of the depositional basin although most of it is produced locally. The heavy pollen producers, which are wind pollinated, are usually overrepresented in the assemblage. Water-transported pollen may constitute a significant fraction (Birks & Birks, 1980, p. 179). Additionally, some leaves do not preserve well, e.g. *Quintinia*, which is highly underrepresented in the leaf litter although it is relatively common along streams (Christophel, pers. comm.). Some pollen does not preserve, e.g. the Lauraceae, an important family in some parts of Australia. These differences result in apparent discrepancies between the interpretations from macrofossil and from palynological evidence. However, these two lines of evidence are complementary, not in competition, and when they can be integrated into one paleobotanical interpretation a more balanced and complete story will emerge.

Another important bias results from the conditions necessary for the preser-

vation of plant remains, viz., the anaerobic swamps, bogs, lake bottoms. Such requisites are abundant in high rainfall areas but exceptional under a dry climate or a strong seasonal drought. Consequently, the paleobotanical record is largely that of the wetter climates.

The level of identification in the fossil record is quite variable, particularly for pollen. Fossil populations are easily identified, but they rarely coincide with extant populations. Thus the fossil type may be found in several related genera but not necessarily in all species. Frequently, identifications can be made only to the family or a higher level.

A reliable age for the fossils is essential, but dating is frequently a problem. Many of the fossiliferous deposits are isolated and thin, and palynology is often the only means available for dating such deposits, with consequent dangers of a circular argument. The ages of some deposits are still being debated.

TAXA IDENTIFIED IN THE AUSTRALIAN TERTIARY

The list below includes pollen and macrofossils. The older macrofossil work which based identifications on gross morphology only is considered as unreliable and not included here. For references to the older work, see Duigan, 1950. Cookson and her co-workers consistently used epidermal and other cellular detail as confirmation of identifications. Their work and that of subsequent authors is included here. Botanical names are preferred and the reader is referred to the reference for fossil names and the proof of identification. Taxa listed without a reference have been reviewed in Martin (1978) and this reference is not repeated. Where a taxon has not been reviewed in Martin, 1978, and the fossil name is necessary to follow the literature, then it is included here in brackets. Throughout the rest of the text, fossil names are only used where necessary for clarification. Where there have been taxonomic revisions, only the latest reference is given. Where the identification and Australian occurrence are found in separate references, both are given. The qualifications and suffixes are those used by the original authors, viz.

Type—a good fit with reference material but it may not be restricted to the particular taxon

Comp—compares favorably with existing reference material

Sim—a strong similarity between fossil type and the present day taxon

Like—strong evidence for the identification

No suffix—a reasonably certain identification.

Type of fossil indicated thus:

P—pollen
L—leaves or leafy shoots
C—cones or cone scales of gymnosperms
K—flowers
F—fruits of angiosperms
S—seeds
W—wood.

GYMNOSPERMAE

ZAMIACEAE: *Bowenia* L Hill, 1978; *Lepidozamia* L Hill, 1980.
TAXODIACEAE: *Athrotaxis* L Townrow, 1965b.
CUPRESSACEAE: Cupressaceae P not identified further; *Callitris* sp. L Blackburn, 1981b; three forms related to *Papuacedrus* L Offler, 1969.
PODOCARPACEAE: *Phyllocladus* P & L Cookson & Pike, 1954, ? W Patton, 1958; *Dacrydium* type 1, *D. franklinii* P; *Dacrydium* type 2, Section B of the genus P, L & S Cookson & Pike, 1953b; three forms of *Dacrydium* related to sections A, B and C respectively L Offler, 1969; *Podocarpus* type 1, section *Dacrycarpus* P & L Cookson & Pike, 1953a, Townrow, 1965a; *Podocarpus* type 1, most other sections in the genus, P & L Townrow, 1965a, L Blackburn, 1981a, at least 5 spp. Blackburn, 1981b; *Microcachrys* P; *Microstrobos* L Townrow, 1965a.
ARAUCARIACEAE: Araucariaceae P not distinguishable to generic level; *Araucaria* L & C Cookson & Duigan, 1951; *Agathis* L & C Cookson & Duigan, 1951, W Patton, 1958.

ANGIOSPERMAE Subdivision DICOTYLEDONAE

WINTERACEAE: *Tasmannia* (= *Drimys*) P.
MORACEAE: Moraceae comp P Luly et al., 1980.
FAGACEAE: *Nothofagus*, the *menziesii* pollen type P; *Nothofagus*, the *fusca* pollen type P; *Nothofagus*, the *brassii* pollen type P.
CASUARINACEAE: *Casuarina* P & F Pike, 1953, W Patton, 1958. Both Cryptostomae and Gymnostomae L & F Christophel, 1980, Blackburn, 1981b.
GYROSTEMONACEAE: Gyrostemonaceae P Luly et al., 1980.
PORTULACACEAE: *Montia* P.
CHENOPODIACEAE/AMARANTHACEAE: P of Chenopodiaceae and some Amaranthaceae are indistinguishable.
POLYGONACEAE: *Polygonum* pantoporate pollen type (Martin, unpubl.).
ELAEOCARPACEAE: *Elaeocarpaceae* F Blackburn, 1981b; *Elaeocarpus* P Luly et al., 1980.
BOMBACACEAE: Bombacaceae (*Bombacacidites bombaxoides*) P Couper, 1960, Stover & Partridge, 1973.
MALVACEAE: Malvaceae P.
ERICACEAE/EPACRIDACEAE: Ericaceae/Epacridaceae P is very similar.
SAPOTACEAE: Sapotaceae P not identified further.
EVENACEAE: Ebenaceae aff. *Diospyros* K & L Christophel, 1981b.
SYMPLOCACEAE: *Symplocos* P.
EUCRYPHIACEAE/CUNONIACEAE (dicolpate): *Geissois-Eucryphia* comp P Luly et al., 1980; *Ceratopetalum* comp P Luly et al., 1980.
CUNONIACEAE (tricolporate): Cunoniaceae P Luly et al., 1980.
ESCALLONIACEAE: *Polyosma* sim P Luly et al., 1980; *Quintinia* P.
MIMOSACEAE: *Acacia* P & L Cookson, 1954.
LEGUMINOSAE (= PAPILIONACEAE): Leguminosae P Luly et al., 1980.
HALORAGACEAE: *Haloragis* P; *Myriophyllum* P.
GUNNERACEAE: *Gunnera* P.
MYRTACEAE: Seven pollen types not reliably identifiable further, *Acmena* comp Luly et al., 1980; *Baeckea* comp Luly et al., 1980; *Rhodamnia* comp Luly et al., 1980; *Syzygium-Cleistocalyx* comp Luly et al., 1980; *Eucalyptus*-like F Lange, 1978a; *Leptospermum*-like F Lange, 1978a; *Calothamnus*-like F Lange, 1978a; F like *Melaleuca-Callistemon* Lange, 1978a; *Angophora*-like F Lange, 1978a.
ONAGRACEAE: *Jussiaea* (*Corsinipollenites*) P Traverse, 1955, Hekel, 1972; *Fuchsia* P, A. D.Partridge, pers. comm., D.Hos, pers. comm.
PROTEACEAE: *Adenanthos*-type P. TRIBE BANKSIEAE P & L Cookson & Duigan, 1950, L Blackburn, 1981a, 6 spp. of L Blackburn, 1981b; *Banksia* P Luly et al., 1980, F Cookson & Duigan, 1950, Pike, 1953, W Patton, 1958; *Beauprea* P TRIBE GREVILLEAE L Blackburn, 1981a; *Grevillea*-type P; *Helicia*-type P; *Isopogon*-type P; *Orites* comp P Luly et al., 1980; *Xylomelum*-type P; *Xylomelum* comp P Luly et al., 1980; Proteaceae comp P Luly et al., 1980. Many pollen forms attributed to the family have not been identified further. cf. Proteaceae I, II, III and IV L Lange, 1978b.
RHIZOPHORACEAE: Rhizophoraceae (*Zonocostites ramonae*) P Germeraad et al., 1968, Hekel, 1972.
ALANGIACEAE: *Alangium* (*Alangiopollis*) P Traverse, 1955, Hekel, 1972.
OLACACEAE: *Anacolosa* P.
SANTALACEAE: *Santalum* P.
LORANTHACEAE: *Amylotheca* P; *Decaisnina*-type P; Loranthaceae P Luly et al., 1980.
AQUIFOLIACEAE: *Ilex* P.

EUPHORBIACEAE: *Austrobuxus-Dissiliaria*, the spiny type P; *Austrobuxus-Dissiliaria*, the non-spiny type P; *Choriceras* comp (non-spiny) P Luly et al., 1980; *Austrobuxus* (= *Longetia*) (spiny) P Luly et al., 1980; *Coelebogyne* P; *Macaranga-Mallotus* P; *Micrantheum-Neoroepera* P; *Omalanthus* comp P Luly et al., 1980; *Petalostigma* P; Euphorbiaceae P Luly et al., 1980.
RHAMNACEAE: Rhamnaceae P Luly et al., 1980.
VITACEAE: Vitaceae P Luly et al., 1980.
SAPINDACEAE: Tribe Cupaniae P; *Diplopeltis* P; *Dodonaea* P; *Dodonaea* cf. *D. triquetra* P, Martin unpub.
RUTACEAE: *Melicope* comp P Luly et al., 1980; Rutaceae P Luly et al., 1980.
GERANIACEAE: *Geranium* P; *Pelargonium* P.
POLYGALACEAE: Polygalaceae P.
ARALIACEAE: Araliaceae P Luly et al., 1980; between *Fatsia* and *Harmsiopanax* L Blackburn, 1981a.
GENTIANACEAE: *Gentiana* sim P Luly et al., 1980.
OLEACEAE: Oleaceae P & L Cookson, 1947; *Jasminum* comp P Luly et al., 1980.
RUBIACEAE: '*Randia*' *chartacea* type P.
COMPOSITAE: Compositae P.

ANGIOSPERMAE Subdivision MONOCOTYLEDONAE

RESTIONACEAE: *Hypolaena*-type (with centrolepidoid pore) P; *Restio*-type (with graminoid pore) P; Restionaceae/Centrolepidaceae P Luly et al., 1980.
CYPERACEAE: Cyperaceae P not identified further.
GRAMINEAE: Gramineae P not identified further.
SPARGANIACEAE: *Sparganium* P; *Sparganium*-type 2 P.
PALMAE: *Nypa* (*Spinozonocolpites prominatus* = *S. echinatus*) P Muller, 1968, Stover & Evans, 1973, Hekel, 1972.
LILIACEAE: *Rhipogonum* comp P Luly et al., 1980; Liliaceae comp P Luly et al., 1980.

FIRST APPEARANCES, SOUTHEASTERN AUSTRALIA

The first appearance and approximate time range of the Tertiary taxa are shown in Fig. 8. Some gymnosperms extend from the middle Mesozoic through the Tertiary. The first angiosperm that can be reliably identified with a modern taxon is *Ilex* (Martin, 1977b). Other angiosperms that first appear in the late Cretaceous are *Nothofagus* and the proteaceous type. The Myrtaceae, perhaps the most important family in Australia today, is first seen in the Paleocene. Taxa appear almost continuously through the Tertiary. In the late Tertiary, there are more herbaceous taxa making their first appearance. It is not known whether the first appearances are the result of evolution or migration (probably a mixture of both).

QUANTITATIVE ASPECTS, SOUTHEASTERN AUSTRALIA

The quantitative aspects through the Tertiary of the major pollen types grouped according to their taxonomic affinities are shown in Fig. 9. As well as the abundant pollen types, there are many other types only found in low frequencies and not shown in Fig. 9. A detailed interpretation and the methods involved are discussed in Martin, 1978. The main points are summarized here:

Paleocene. The gymnosperm group, consisting of ten different pollen types is most abundant in the oldest of the assemblages. The proteaceous group, which may consist of up to 23 different pollen types, is also abundant. Many of these proteaceous types become extinct during the Tertiary. Myrtaceae is present but not abundant. *Nothofagus* is present only in low frequencies. Judging from the present day pollen dispersal behavior of *Nothofagus* (Martin, 1978), these low

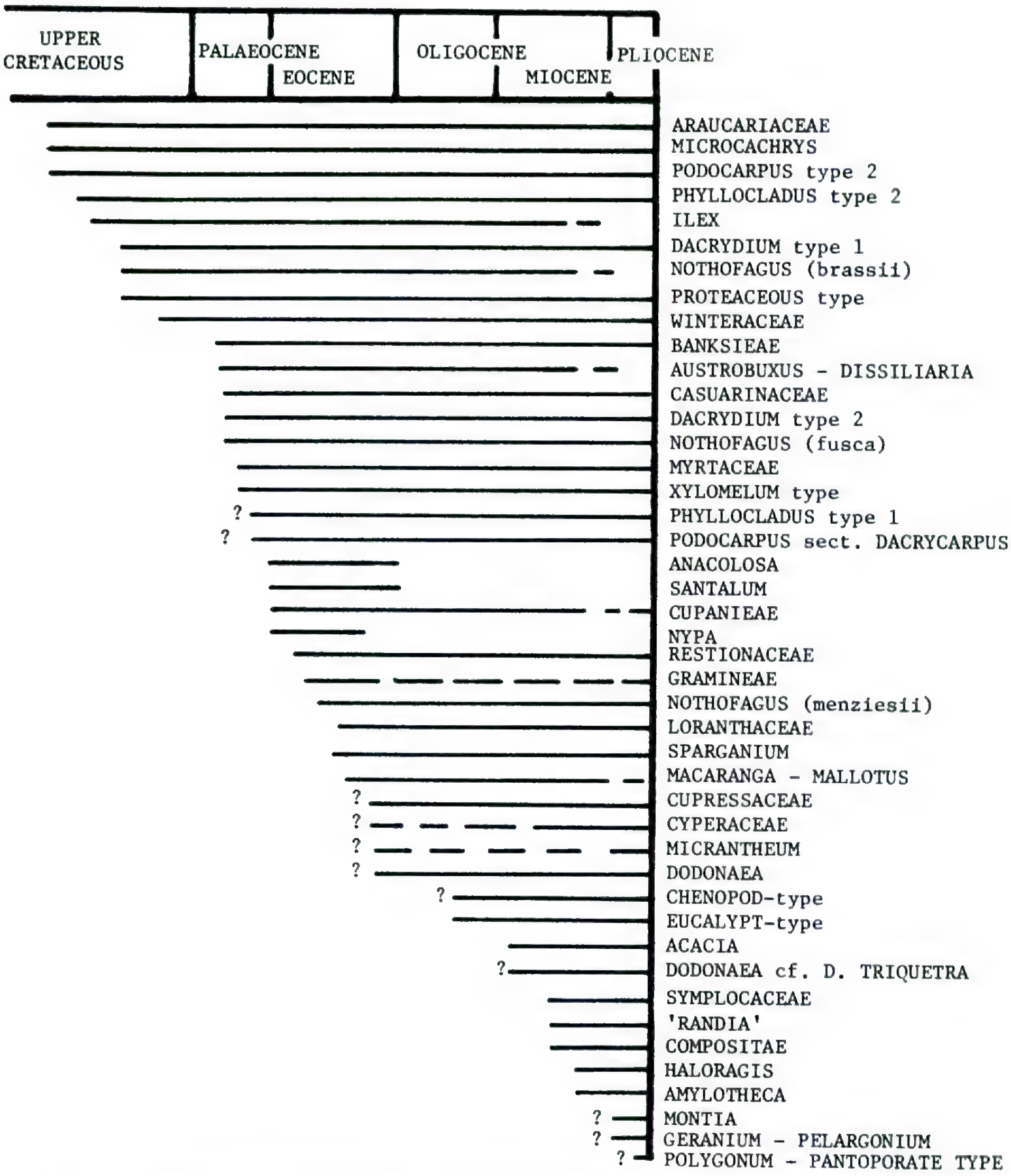

FIGURE 8. Range chart showing the first appearances of fossil pollen taxa through the Tertiary, for southeastern Australia. Modified from Stover and Partridge, 1973, and Martin, 1978.

frequencies probably indicate that it was not very common and growing at some distance from the areas of deposition. Angiosperms other than these major groups continue to diversify.

Eocene. The early Eocene assemblages are generally like those of the Paleocene, there is a marked change about mid-Eocene time when *Nothofagus* becomes the dominant pollen group. This great increase in *Nothofagus* must represent an increase in this taxon in the vegetation, but not to the extent suggested by the pollen frequencies, because *Nothofagus* is a very heavy pollen producer. Many of the proteaceous types and some other angiosperms became extinct during the mid-late Eocene.

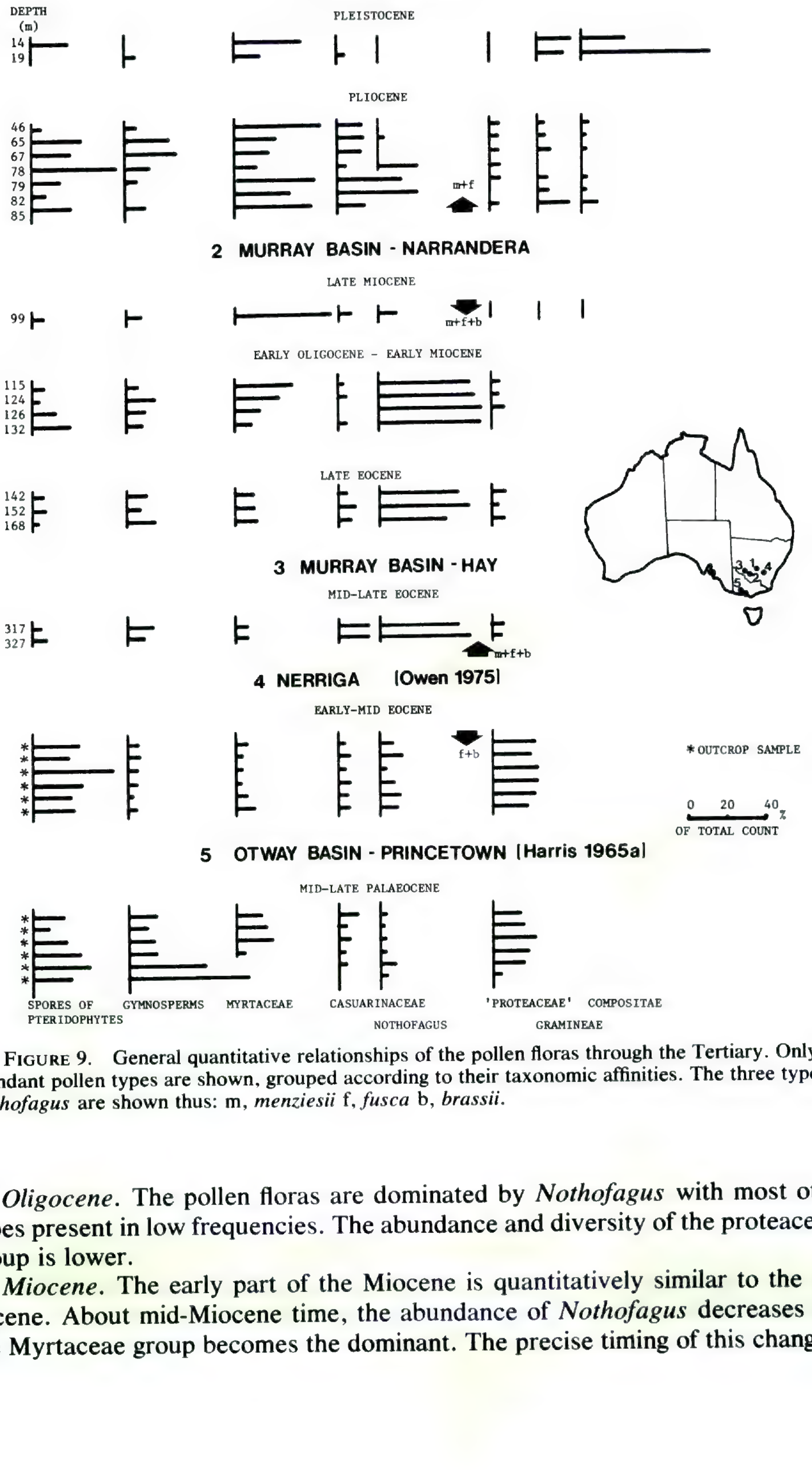

FIGURE 9. General quantitative relationships of the pollen floras through the Tertiary. Only the abundant pollen types are shown, grouped according to their taxonomic affinities. The three types of *Nothofagus* are shown thus: m, *menziesii* f, *fusca* b, *brassii*.

Oligocene. The pollen floras are dominated by *Nothofagus* with most other types present in low frequencies. The abundance and diversity of the proteaceous group is lower.

Miocene. The early part of the Miocene is quantitatively similar to the Oligocene. About mid-Miocene time, the abundance of *Nothofagus* decreases and the Myrtaceae group becomes the dominant. The precise timing of this change is

earlier inland and later near the southeast coast. There are 8 different pollen types in the Myrtaceae group, but these cannot be identified reliably with extant genera in the family. The 'eucalypt pollen type,' which may be found in other genera besides *Eucalyptus*, is present but not abundant. The greater proportion of the Myrtaceae pollen is more like that found in *Tristania*, *Backhousia*, *Baeckea*, *Syzigium*, and *Acmena* (and possibly other genera). Molds and casts of fruits that are like *Eucalyptus*, *Leptospermum*, *Calothamnus*, *Melaleuca-Callistemon*, and *Angophora* (Lange, 1978a) show these genera exist in the fossil record, but they can only be dated as Eocene-Oligocene or Miocene (Ambrose et al., 1979).

Pliocene. Myrtaceae is dominant, although there are small amounts of *Nothofagus* and a few of the early Tertiary pollen forms are still present. Gramineae and Compositae are usually present but in low frequencies.

Pleistocene. *Nothofagus* and most of the gymnosperms have disappeared from most of the Australian continent. Myrtaceae continues as the dominant and abundance of Gramineae and Compositae have increased greatly. For further detail of the Quaternary, see Kershaw, 1981.

As well as these abundant groups, there are many pollen types found only in low frequencies (about 5% or less). These types probably come from plants with a low pollen production and insect pollination, e.g. *Acacia*, which is important in the vegetation today. Thus a consistent presence of a low frequency taxon is thought to indicate that it may have been important in the vegetation. Many of these low frequency taxa show changes about the time of change in the dominant groups.

These quantitative relationships must represent vegetation that was closed forest through most of the Tertiary, judging from the low herbaceous content (Gramineae and Compositae). A physiognomic analysis of some Eocene leaf floras of southeastern Australia shows them to be most similar to Simple Mesophyll Vine Forest, Complex Notophyll Vine Forest, and Simple Notophyll Vine Forest. These forest types are found today in the rainforest along the east coast of Australia between the latitudes of 15°S–25°S, 20°S–35°S and 15°S–37°S (at higher altitudes), respectively (Christophel, 1981a). The modern rainforests are classified into these physiognomic types on the size of mature, exposed, 'sun' leaves from the tree layers only (Webb, 1959). Fossil leaf floras would contain some of the larger 'shade' leaves, which would inflate the perception of tropicality/subtropicality. However, the diversity of angiosperms represented suggests a complexity now found only under warmer conditions, and certainly not in temperate forests (Webb et al., 1982). If the Eocene pollen and leaf floras are compared, then the latter indicate a much greater diversity in the flora (Christophel, 1981b), but this may be a reflection of the regional versus local representation, respectively, of the two types of fossils.

The nature of these closed forests change through the Tertiary, but it is not until the Pliocene that the forest started opening up to allow the development of a herbaceous stratum of Gramineae and Compositae, at least in southeastern Australia. Open woodlands and/or grasslands did not develop until the Pleistocene (Martin, 1978) in southeastern Australia although the timing of this major change in the vegetation is earlier in inland regions and in Queensland (discussed more fully below).

VARIATION IN THE TERTIARY FLORAS

The general quantitative relationships of the Tertiary floras shown in Fig. 9 are usually recognizable in pollen assemblages of the same age. However, this does not imply that the vegetation was more uniform than that of today. Attempts to identify pollen assemblages from surface samples of moss polsters, surface lake muds, etc., with the parent vegetation have shown that they are identifiable at the "vegetation-landform unit" level, i.e. large vegetation units. When individual plant associations are sampled, little distinction could be made below the level of vegetation-landform unit (Birks & Birks, 1980, p. 243). Consequently, these Tertiary pollen assemblages shown in Fig. 9 should be viewed in the light of large vegetation units. However, with the use of improved methods, more precision in identifying plant communities in the fossil assemblages is possible (see Luly et al., 1980). Even so, when sufficient samples of the same age are compared, they reveal some time-related and geographic variation in the Tertiary floras, although the problems of dating (discussed previously) should be remembered.

Mid-late Eocene Comparisons. Figure 10 compares four mid- and late Eocene assemblages. Three sites are late Eocene, one (St. Vincent's Basin) is mid-Eocene. Figure 10 shows that the spores of pteridophytes are less frequent in inland locations. Trapping of modern pollen has shown that fern spores form a greater proportion of the catch from water transport than from aerial transport (Birks & Birks, 1980). Narrow gullies are more favorable habitats for ferns, so there may be other environmental reasons besides climate for these differences. Only Albany would have been coastal-oceanic (or near coastal) on Eocene paleogeography. Casuarinaceae may have been more abundant elsewhere in Australia with up to 62% in one sample of the Officer Basin. It is not possible to distinguish *Gymnostoma* from *Casuarina* on pollen morphology (Kershaw, 1970a). If Casuarinaceae grew in or along the margins of the swamps or lakes, then it could produce a higher pollen representation. *Nothofagus* may have been more abundant in southeastern Australia, particularly when the Murray Basin is compared to the Officer Basin. The low values in the St. Vincent's Basin are not strictly comparable for these may pre-date the mid-Eocene rise in abundance of *Nothofagus*. Similarly, the high values of 'Proteaceae' in St. Vincent's Basin may predate the mid-late Eocene decline of this group, but the high values of 'Proteaceae' at Albany are unusual for the late Eocene (Hos, 1975, 1977, 1978; and Martin, 1978).

Variation in Late Eocene to Early Miocene Assemblages Eastern Murray Basin. Numerous bores penetrating strata of this time range have been studied. Figure 11 shows one of the gymnosperms, the *Dacrydium franklinii* pollen type (= *Phyllocladidites mawsonii*) plotted as a ratio of the total gymnosperms count alongside the percentage of gymnosperms in the total pollen count. While the percentage of total gymnosperms does not vary much, the relative proportions of the different gymnosperms may change. In the late Eocene–early Oligocene, *Dacrydium franklinii* is the most common single gymnosperm pollen type in the group. A rise in abundance of *D. franklinii* may be seen in the Gippsland Basin of southeastern Victoria where this pollen type may constitute up to 80% of the total count in some late Eocene–early Oligocene coals (Stover & Partridge, 1973). Figure 12

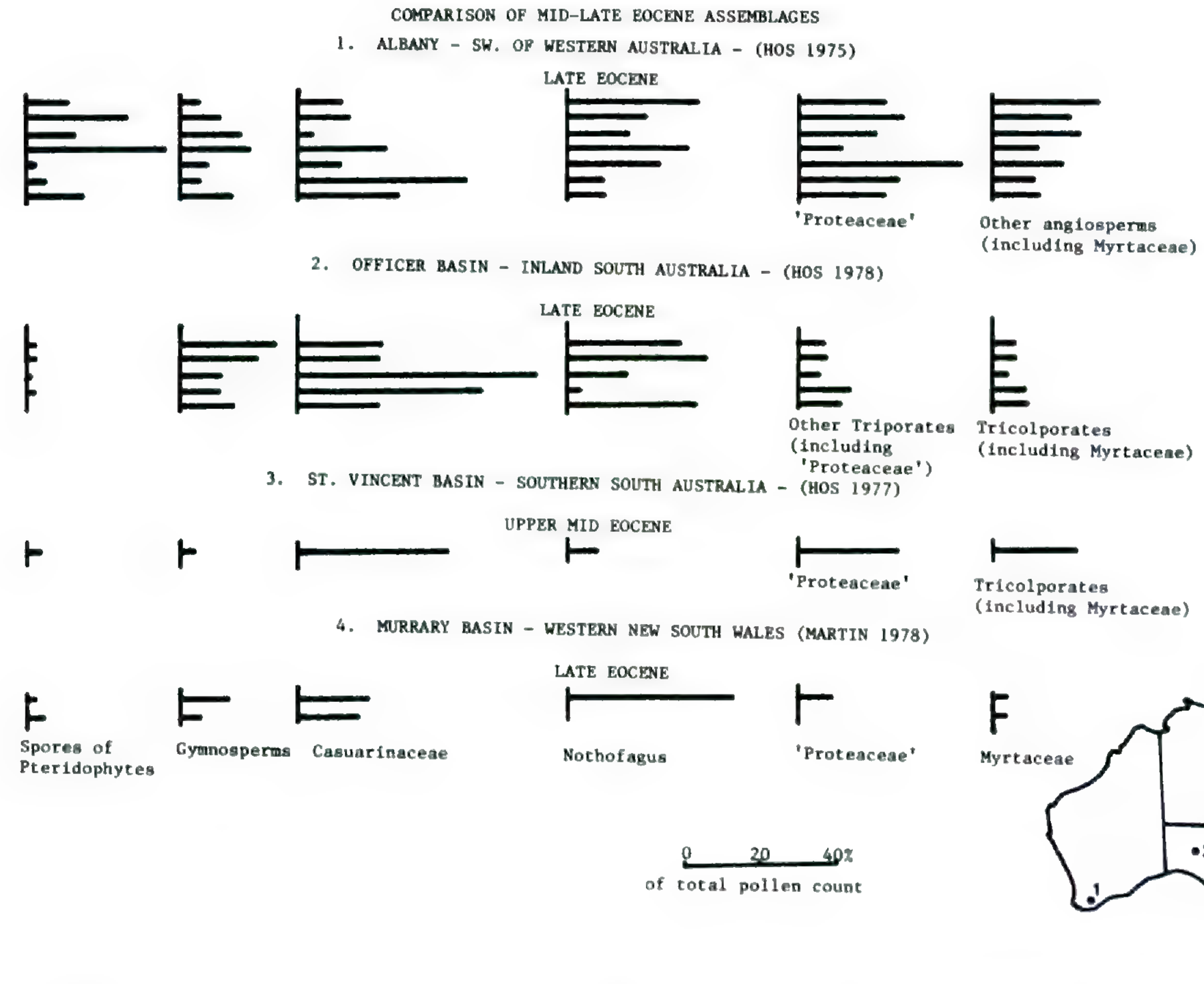

FIGURE 10. Comparison of the abundant pollen groups, in the mid-late Eocene. Spores of pteridophytes and 'Proteaceae' are more abundant at Albany. Casuarinaceae is less abundant in the Murray Basin, the easternmost location.

shows one of the *fusca* pollen type, *Nothofagus flemingii,* plotted in the same way. While the percentage of the *Nothofagus* group varies little, *N. flemingii* shows two peaks of greater abundance, one in the early Oligocene and the other probably in the early Miocene. These two peaks in *N. flemingii* abundance may be recognized in the same stratigraphic position over the whole area studied. These examples illustrate how the grouping of the taxa in Fig. 9 may mask the variation present.

The ratio of Myrtaceae to *Nothofagus* pollen is presented in Fig. 13 and shows a gradual increase where the sampling interval is sufficiently close. This increase in Myrtaceae is earlier and more marked in bores to the west than those in the south and east of the study area, which is approximately 250 km × 250 km (Martin, unpubl.).

Mid-late Miocene Comparisons. Figure 14 shows that the Myrtaceae reaches the highest values in the Castlereagh River Valley and Jemalong Gap—the two most westerly locations. Latrobe Valley in the most southeastern part of Australia has lower values for Myrtaceae. A reciprocal pattern is seen with *Nothofagus*, highest in the southeast and it has practically disappeared from Queensland. In the Latrobe Valley, two definite habitats may be identified in the coals; (1) open water, which accumulates mainly wind blown pollen and especially *Nothofagus* and (2) swamp, accumulating pollen from the plants on site as well as wind blown

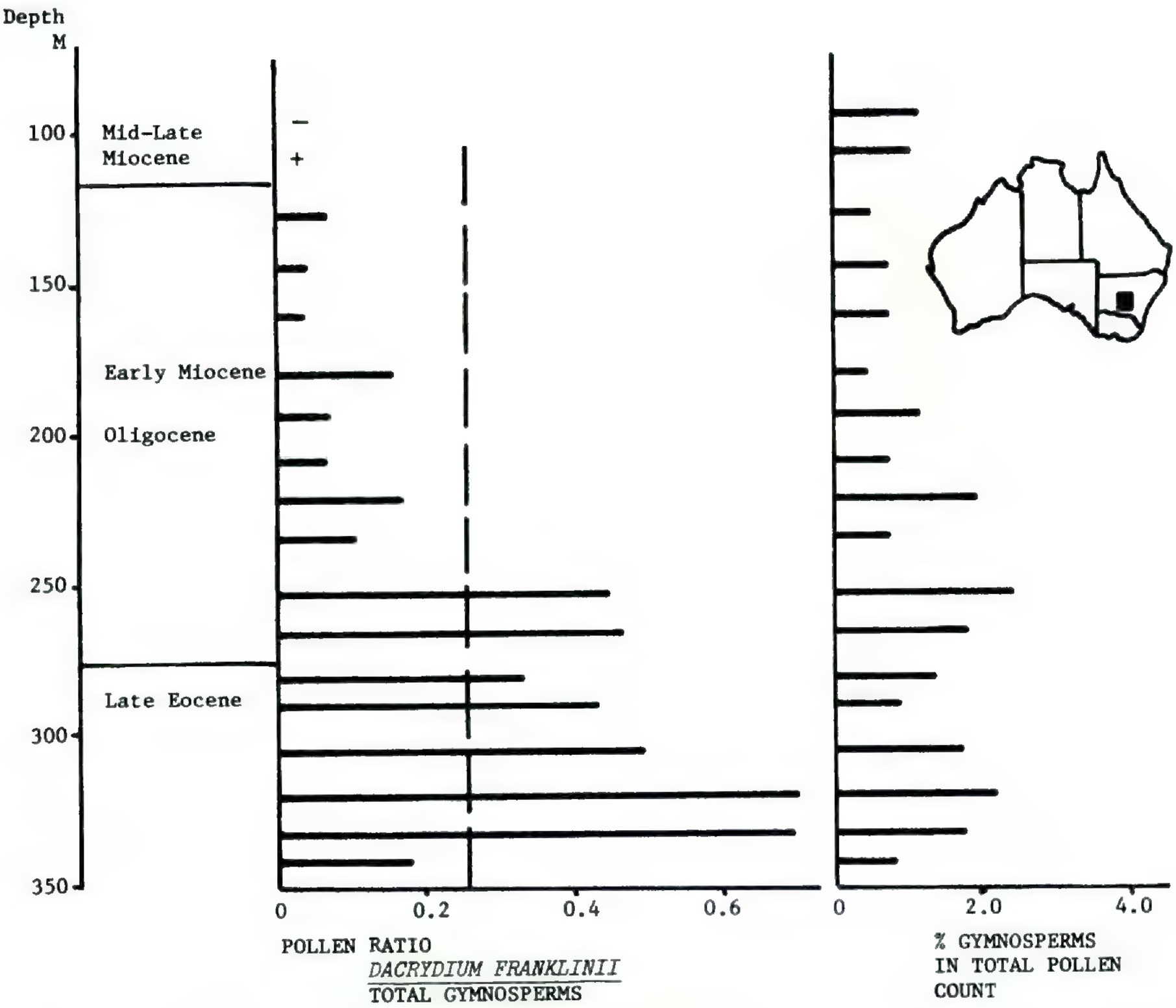

FIGURE 11. The ratio of *Dacrydium franklinii* to total gymnosperms. While the percentage of gymnosperms varies little, *D. franklinii* is the most abundant in the late Eocene–early Oligocene.

pollen. The latter has appreciable quantities of Restionaceae/Centrolepidaceae pollen (Luly et al., 1980). Macrofossils indicate a sclerophyllous vegetation in these swamp habitats (Blackburn, 1980). Assemblages from the Namoi and Castlereagh River Valleys may be very rich in unidentified tricolpate/tricolporate pollen types. Most of the taxa that can be identified in the latter sites are found today on the east coast of northern New South Wales and it is thought that the late Miocene vegetation here was more akin to the subtropical rainforest (Martin, 1980, 1981). Compositae, Gramineae, and the chenopod pollen type (Chenopodiaceae and Amaranthaceae) are present in low frequencies to the north.

Pliocene Comparisons. Figure 15 shows that the Myrtaceae was more abundnat to the west, in Jemalong Gap. Gymnosperms may be quite abundant and particularly the Araucariaceae, which may reach 50% of the total count on the Mooki River Valley. It is not clear whether the Araucariaceae was abundant in the Queensland site, for there is a problem of identification with the fossil pollen type *Dilwynites granulatus*, which may belong to the Araucariaceae but is also like *Cinnamonum* (Harris, 1965a). It is thought that these assemblages with high Araucariaceae are akin to the present day low microphyll vine forests with emergent *Araucaria* ('hoop pine scrubs') of southeastern Queensland. There is a little *Nothofagus* in the Pliocene, mostly the *menzeisii* and *fusca* pollen types. The

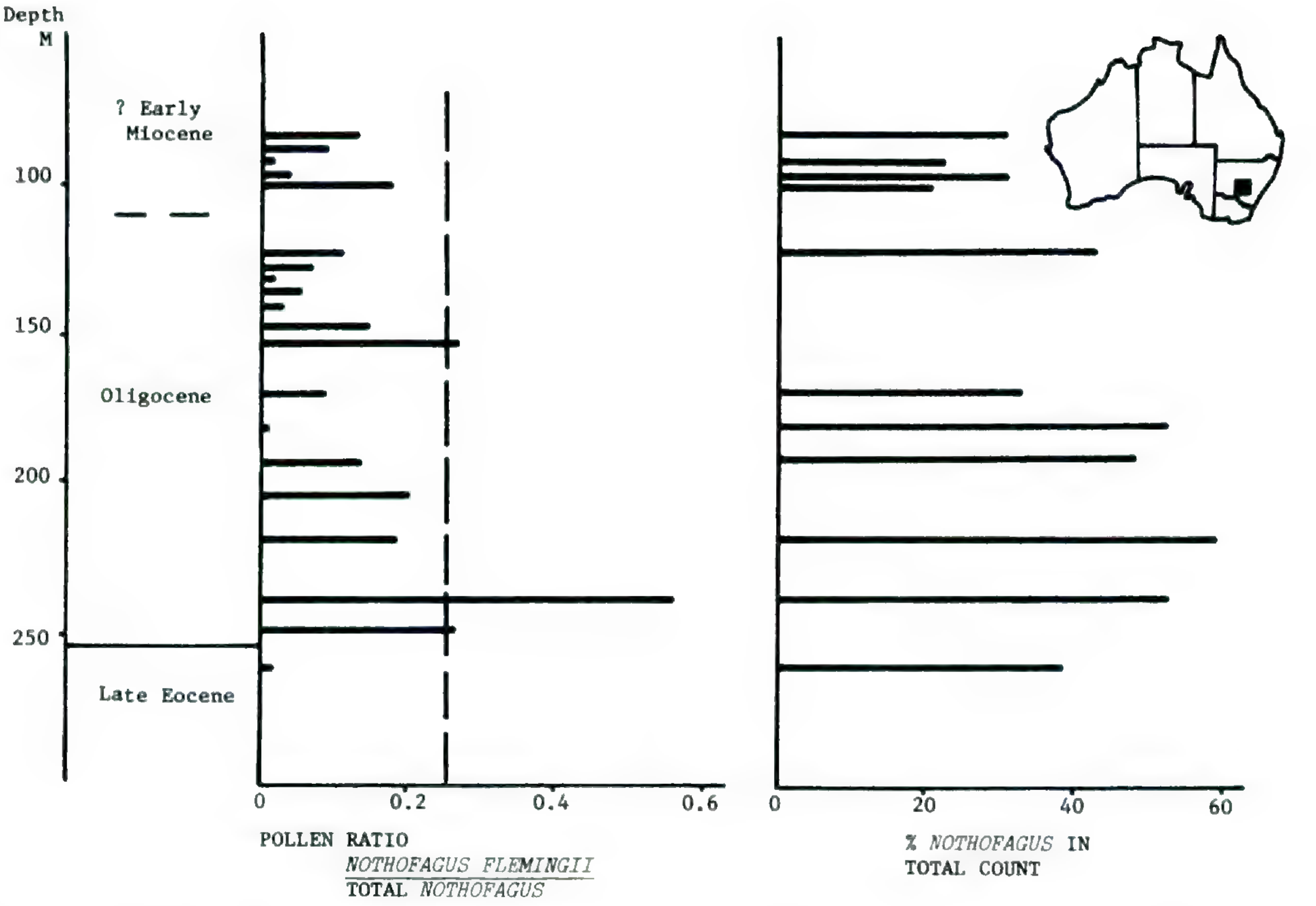

FIGURE 12. The ratio of *Nothofagus flemingii* to total *Nothofagus* pollen. There are two peaks where the ratio exceeds 0.25, indicating change within the *Nothofagus* flora.

brassii type, which accounts for the greatest proportion of the *Nothofagus* count up to the mid-Miocene, is occasionally present but in very minor amounts, 1–2%. Such small quantities could result from long distance dispersal or reworking of the older Tertiary sediments. *Nothofagus* in the Pliocene may be traced over most of southern New South Wales where it forms a valuable stratigraphic datum plane, but it is rarely encountered in the northern regions (Mooki and Castlereagh River Valleys). Compositae may be abundant, particularly to the north. The samples from Jemalong Gap with the high Compositae may be close to the Pleistocene boundary, judging by their distance above the *Nothofagus* horizon. Gramineae is usually present but not abundant and the chenopod pollen type is more abundant in the Queensland assemblage. In southwestern Australia, Myrtaceae or Casuarinaceae may be abundant. Restionaceae is usually well represented and *Gyrostemon* is important in some samples. Pteriodophytes and gymnosperms are rare.

Other reports give further indication of variation across Australia at different time intervals during the Tertiary. A pollen flora from Central Australia, 170 km northwest of Alice Springs, is reported to be mid-late Eocene in age by Kemp (1976). It has many features in common with those of southeastern Australia, but there are some differences. Cupressaceae, Cyperaceae, and *Micrantheum*, which are found in the Central Australian assemblages (Kemp, 1976), are rarely seen in southeastern Australia until the late Miocene–Pliocene. Early-mid Miocene assemblages near Lake Frome in inland Australia contain abundant grass pollen and have been interpreted as representing riverine rainforest with grasslands or

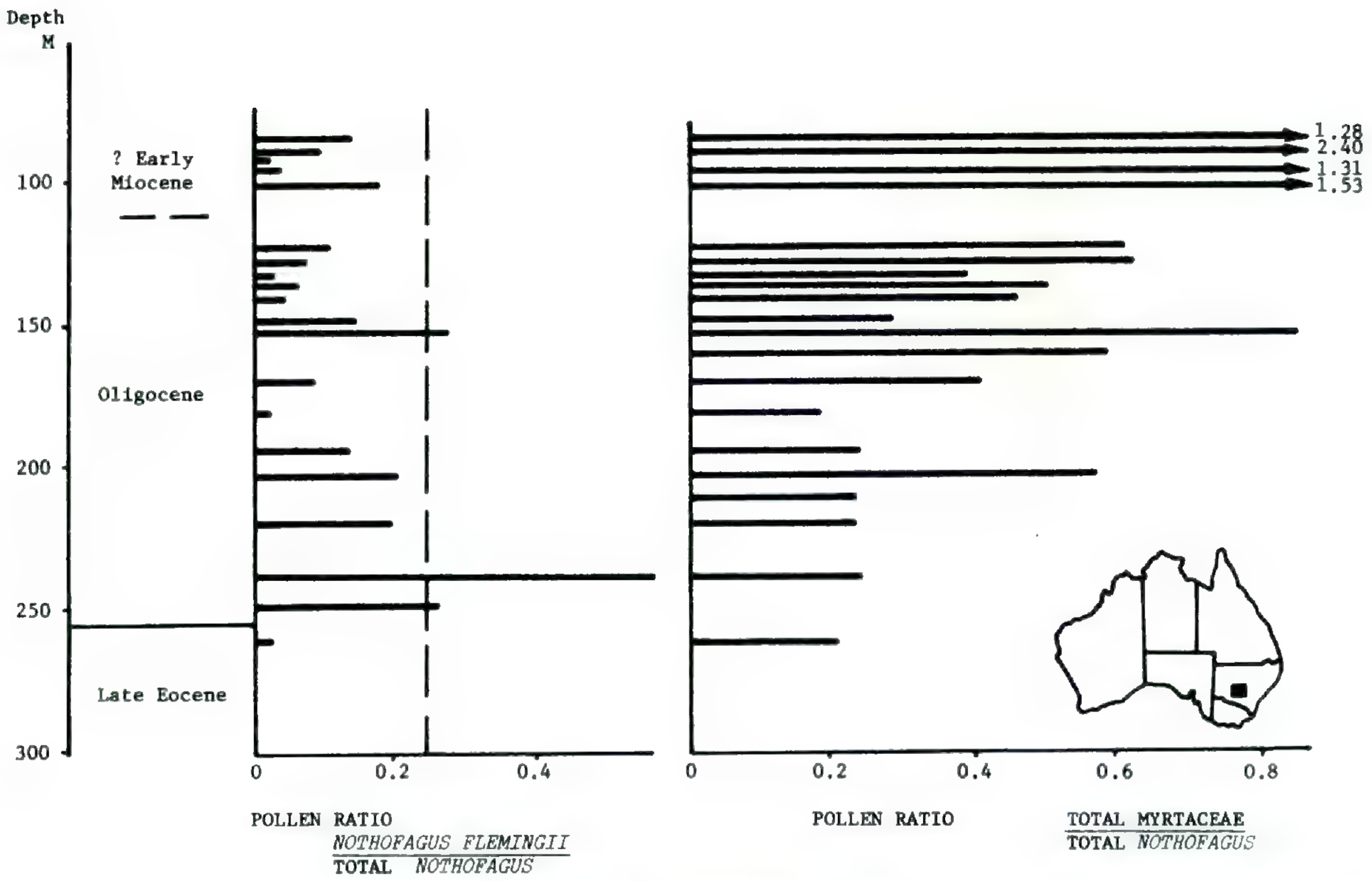

FIGURE 13. The ratio of Myrtaceae to *Nothofagus* pollen. There is an increase in the early Miocene, indicating a replacement of *Nothofagus* by Myrtaceae as the abundant pollen type.

grassy woodlands on the drier slopes and hillsides (W. K. Harris, pers. comm. in Callen & Tedford, 1976). This contrasts with southeastern Australia where grasslands did not develop until the Pleistocene (Martin, 1969). These Central Australian records probably indicate the early stage of desiccation and contraction of closed forests. Unfortunately, once a dry climate or a strong seasonal climate is established, the permanently wet bogs, lakes, etc., which are necessary for preservation of plant material, disappear so there is no record of the development of the arid flora.

Queensland assemblages have been compared with others where relevant, but there are other differences as well. *Anacolosa* and *Santalum* pollen types, which disappear from southeastern Australia by the end of the Eocene, are found in early Miocene assemblages in Queensland. *Nothofagus* does not become abundant until early Miocene time, and the peak is short lived. It is thought that this Miocene peak is associated with a climatic change or uplift (Hekel, 1972) and suggests that the north was not as suitable for *Nothofagus*.

Comparisons with Quaternary Changes. The Tertiary shows the development of the flora and vegetation to roughly the present day status. In contrast to the Tertiary, the Quaternary shows changes within what is essentially the present day flora and vegetation. Nevertheless, these changes have been quite considerable, for while reasonable analogues of the fossil pollen assemblages may be found in the present vegetation, they are not precise and indicate that plant communities of even 10,000 years ago may no longer exist today.

There have been some extinctions on the Australian mainland as well, for example, *Dacrydium* Sect. B (cf. *D. cupressinum*) in northeastern Queensland

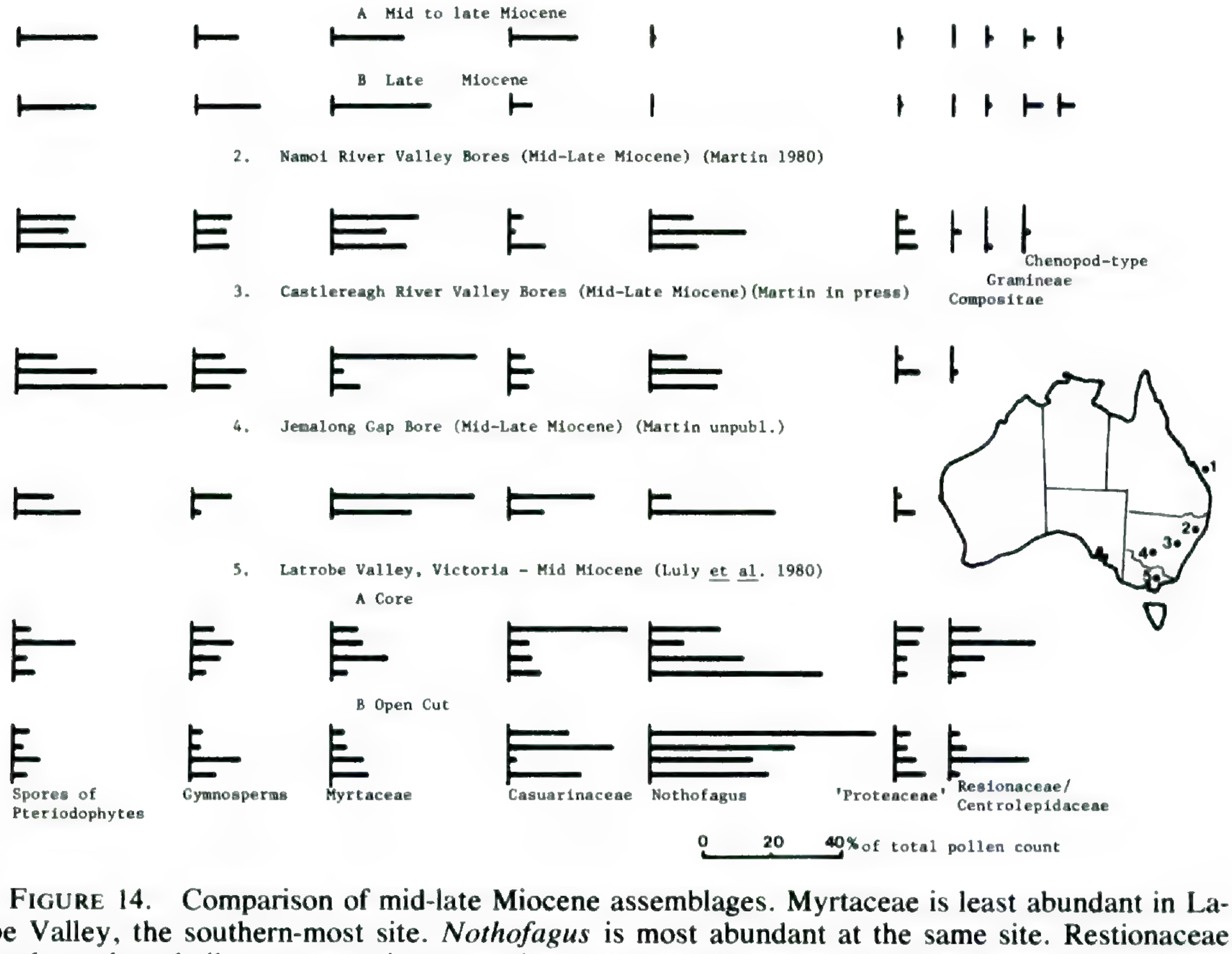

FIGURE 14. Comparison of mid-late Miocene assemblages. Myrtaceae is least abundant in Latrobe Valley, the southern-most site. *Nothofagus* is most abundant at the same site. Restionaceae and other sclerophyllous taxa are important in the Latrobe Valley (see Text for further discussion).

up to about 25,000 years B.P. (Kershaw, 1978), *Dacrydium* Sect. B and *Podocarpus* Section *Dacrycarpus* in northeastern New South Wales, in the Pleistocene (Martin, unpubl.) and *Phyllocladus* in Holocene southwestern Victoria (Dodson, 1974; Churchill & Dodson, 1980). Of the many Quaternary records (Kershaw, 1981), only the two that extend back to the last interglacial period of 125,000 years ago or beyond will be mentioned here.

Lake George in the Eastern Highlands has the longest pollen record of 350,000 years. There are four wooded periods alternating with five non-wooded periods (Singh et al., 1981a, 1981b) and these periods correspond to interglacials and glacials, respectively. The character of the wooded periods changes from wet sclerophyll in the oldest to open sclerophyll and finally dry sclerophyll in the youngest and present wooded period. In an intriguing study of fire history, as reconstructed from the abundance of charcoal particles, fire frequency is always higher in the wooded periods, but increases along with the development of open sclerophyll during the last glacial period. During the non-wooded period of the last interglacial, the fire frequency does not drop, unlike the preceding three non-wooded periods, and this is attributed to Aboriginal man's activities (Singh et al., 1981a).

A record of 123,000 years in northeastern Queensland extends back to the last interglacial period. There is a full cycle of change in which the oldest

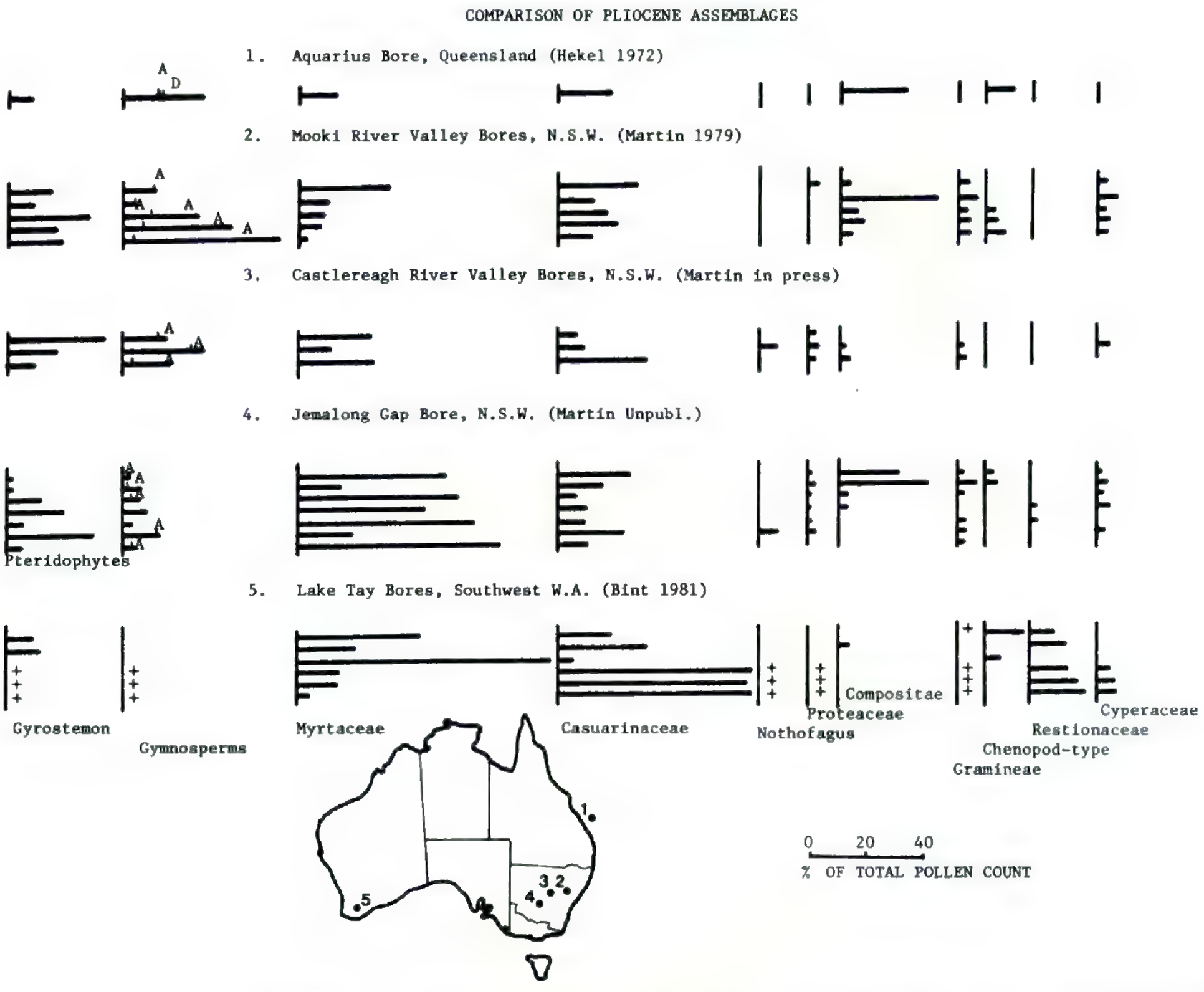

FIGURE 15. Comparison of Pliocene assemblages. A = Araucariaceae; D = *Dilwynites granulatus*; which may have affinities with the Araucariaceae (see Text). Araucariaceae may be abundant in Mooki and Castlereagh River Valleys. Myrtaceae is the most abundant in Jemalong Gap, the western-most site.

and youngest part of the profile are similar, with rainforest angiosperms the major group. The intervening period shows an increase of rainforest gymnosperms then sclerophyllous taxa, with the latter accounting for almost all of the pollen in the sediments of the last glacial period (Kershaw, 1978). The last 20,000 years of this pollen diagram are in agreement with the models proposed by Nix and Kalma (see Fig. 6).

In summary, where the Quaternary record extends back far enough, it shows periods in which two types of vegetation alternate; these periods may be linked with the glacial/interglacial cycles. Vegetation of a drier environment or of a more open nature is always found during the glacial times. The vegetation shows progressive change with the repetition of the cycles. There is some evidence of the effect of man on the vegetation through his penchant for starting fires. The oldest confirmed date for the presence of man in Australia is 32,000 B.P. (Barbetti & Allen, 1972), but he may have been present at 40,000 B.P. or even earlier (Bowler, 1976).

COMPARISONS WITH NEW ZEALAND

Mildenhall (1980) has reviewed the Cenozoic plant biogeography of New Zealand and made comparisons with Australia. The main points are summarized here.

The late Cretaceous floras of Australia and New Zealand are very similar.

The same palynological zones and datum planes may be used. *Nothofagus* appears in the late Cretaceous in Australia, New Zealand, and South America, and is scarce. In the Paleocene, podocarps are very common, all three pollen groups of *Nothofagus* are present but not abundant. Proteaceae, *Casuarina,* and the *fusca* pollen type of *Nothofagus* are the next most common to the podocarps. Myrtaceae appears in the Paleocene. The assemblages are essentially temperate, with rare occurrences of some tropical elements, e.g. *Anacolosa* and palm pollen. The Paleocene floras are similar to those of the late Cretaceous.

The Eocene is a time of widespread change, just as it is in Australia, and many new forms appear. *Nothofagus* becomes dominant, supplanting the podocarps. First the *fusca* group becomes more abundant, followed by the *brassii* group. *Phyllocladus* and pollen of *Podocarpus* section *Dacrycarpus* appear in the Eocene and there is an increased diversity in the Proteaceae and other angiosperms. At the end of the Eocene, the tropical and subtropical elements disappear, e.g. *Anacolosa* and the palms, including *Nypa*.

In the Oligocene, the *brassii* type of *Nothofagus* is dominant, with *Casuarina* often abundant. Myrtaceae, palms, podocarps, and the *fusca* type of *Nothofagus* are also prominent. Although *Dacrydium franklinii* is present, an abundance in the early Oligocene comparable to some of the high values seen in southeastern Australia has not been found in New Zealand. The *Macaranga-Mallotus* pollen type (Euphorbiaceae) may have been locally abundant. There is an increase in temperate taxa and a decrease in species diversity probably as a result of continued cooling.

In the early Miocene, low lying swamps are common in which *Sparganium* and palm pollen are abundant. The flora is very rich, indicating subtropical forests. The assemblages are dominated by the *brassii* type of *Nothofagus,* Myrtaceae (including ? *Eucalyptus*), *Casuarina,* podocarps, and *Macaranga-Mallotus*. The late Miocene shows a dramatic change with many herbaceous taxa appearing (Mildenhall, 1980). *Acacia* also appears in the early Miocene, approximately the same time as its first appearance in Australia (Pocknall, 1981) and temperate taxa become prominent in most assemblages. The *brassii* type of *Nothofagus* is still common and occasionally dominant, as is *Casuarina,* but the *fusca* type of *Nothofagus* and podocarps are more often dominant. Many new taxa appear in the Miocene.

In the Pliocene, a mosaic of different forest types occurs, both in space and time. Glaciation reduces some forests to scrubland or grassland. The *brassii* pollen type of *Nothofagus* is still prominent in the north. Palm pollen ceases to be important in the early Pliocene. Ferns become more diverse and abundant. In the South Island, middle Pliocene assemblages contain abundant grasses, Compositae, and other herbaceous taxa, indicating grassland. There is, however, a wide range of floral characteristics indicating rapid environmental change. Many tropical taxa disappear during the Pliocene. Many of the taxa appearing in the Miocene disappear before the Pleistocene glaciations. A number of shrubby and herbaceous taxa appear, including *Acacia,* which disappears from New Zealand in the Pleistocene. In the Pleistocene repeated glaciations wipe out many taxa.

Mildenhall (1980) also cited a number of examples of trans-Tasman migration. One of the best examples is seen in the different pollen types of *Nothofagus*.

TABLE 1. Comparison of first appearances in Australia and New Zealand.

Taxa Appearing First in Australia	First Appearance	
	Australia	New Zealand
Ilex	Late Cretaceous	Eocene
Nothofagus flemingii	Paleocene	Late Eocene
N. falcata	Mid-Eocene	Oligocene
Polycolpites reticulatus	Early Eocene	Late Eocene
Restionaceae, '*Restio*' pollen type	Early Eocene	Mid-Eocene
Micrantheum	? Eocene[1]	Late Mio-Pliocene
Macaranga-Mallotus	? Eocene[2]	Oligocene
Polygalaceae (*Polycolpites esobalteus*)	Early Eocene	Miocene
Banksia	Early–mid-Paleocene	Late Eocene
Bombacaceae (*Bombacacidites bombaxoides*)	Early Eocene	Late Eocene
Cyperaceae	? Eocene	Oligocene
Cunoniaceae	Eocene[3]	Oligocene
'*Randia*' *chartacea*	Mid-late Miocene	Early–mid-Pliocene

Taxa Appearing First in New Zealand	First Appearance	
	New Zealand	Australia
Nothofagus, menziesii type	Paleocene	Early Eocene
Anacolosa	Paleocene	Eocene

Time ranges from Mildenhall (1980), Stover and Partridge (1973), and [1] Kemp (1976), [2] Martin (unpubl.), [3] Christophel (pers. comm.).

Some types appear first in Australia, some first in New Zealand (see Table 1). Because *Nothofagus* has a very limited seed dispersal (see Martin, 1977b), Mildenhall thinks that long distance dispersal has been accomplished by means of viable pollen to a still receptive gene pool (i.e. windblown pollen from Australia fertilized female flowers in New Zealand). Table 1 lists the taxa common to Australia and New Zealand that appear first in Australia and first in New Zealand. Although not all-inclusive, more taxa make their appearance first in Australia than in New Zealand. Work in progress will change some of the time ranges, but the general conclusion that a number of taxa appear first in Australia will probably remain valid (D. Pocknall, pers. comm.). There are many other taxa that appear about the same time in both. As discussed previously, Australia and New Zealand have remained at approximately the same distance apart, 2,000 km, throughout the Cenozoic, although there have been relative changes in latitude.

COMPARISON WITH SOUTHEAST ASIA

The most complete record comes from Borneo. Paleocene-Eocene floras of Borneo are distinctive and 60% have not been recorded outside of Sarawak. Twenty-six percent of the remainder are world wide. Only 11% can be referred to living genera. Nine percent are exclusively pantropical. One pollen type has northern hemisphere affinities. None of the extremely characteristic Australian groups such as *Proteacidites*, *Nothofagus*, or the southern hemisphere gymno-

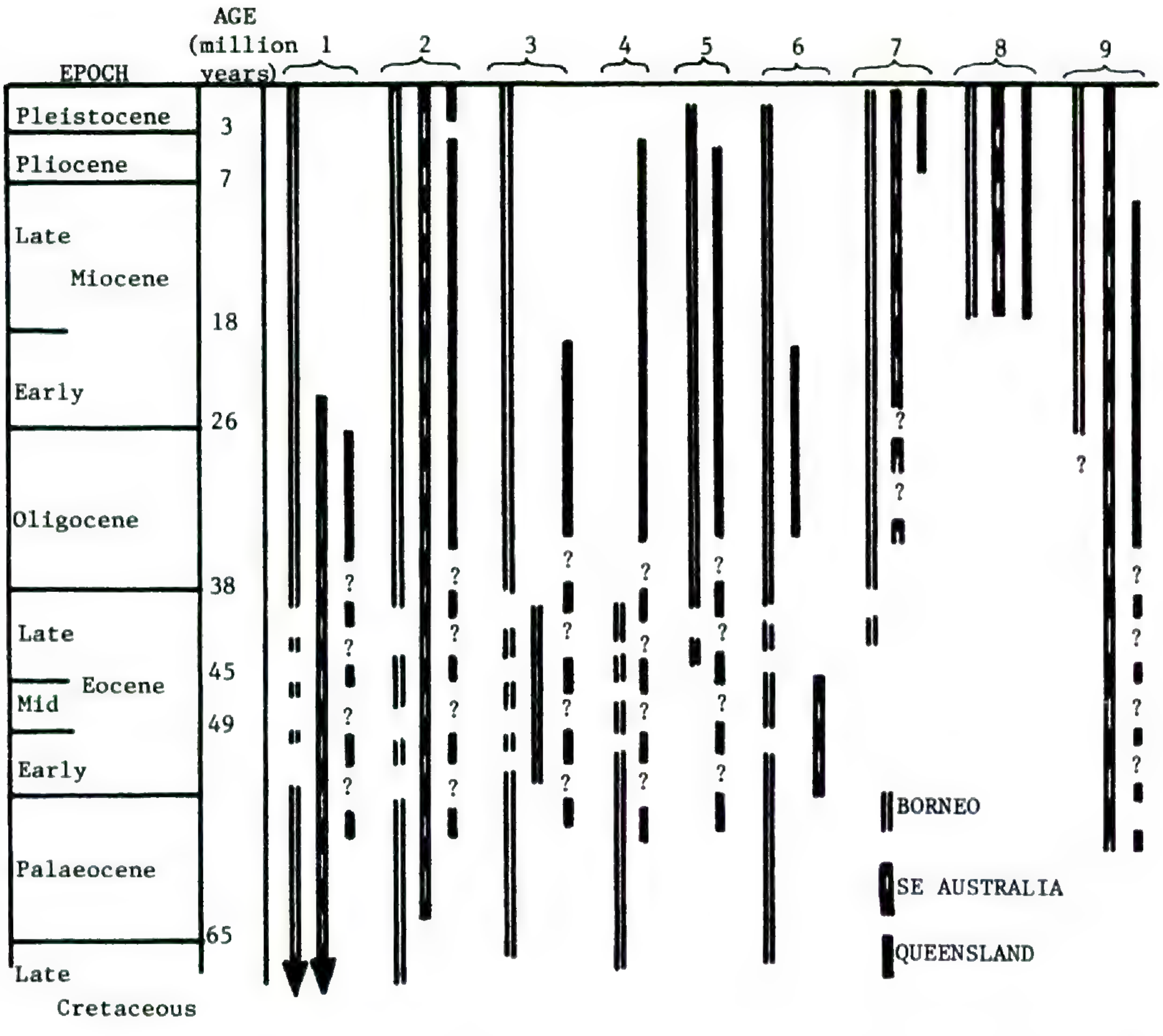

FIGURE 16. Pollen taxa common to Borneo and Australia in the early Tertiary. The broken line for Queensland through the Eocene and into the late Paleocene indicates imprecise dating (see Text for further discussion). The Eocene of Borneo is poorly known (J. Muller, pers. comm.) hence is represented by the broken lines. The numbers represent taxa, see Table 2.

sperms are present. When compared with the latitudinal equivalents in Africa and South America, the Bornean floras are rather depauperate in contrast to the present day, where it has the richest floras (Morley, 1977). Thus the early Tertiary floras of Borneo were very different to those of Australia, as would be expected from the 3,000 km, latitudinally, between the two regions. However, there are a few taxa in common and these are shown in Fig. 16, in which floras of Borneo, Queensland, and southeast Australia are compared (Table 2). Unfortunately, the early Tertiary unit from Queensland is not dated more precisely than Paleocene to Oligocene (Hekel, 1972) (although it probably covers this time range), and this is shown by the broken line on Fig. 16. The *Ilex* pollen type, which has had a world wide distribution since the beginning of the late Cretaceous (Martin, 1977b), is present in Borneo, Queensland, and southeast Australia. Myrtaceae is found in Borneo, Africa, and South America in the Cretaceous (Muller, 1981), before its first appearance in southeast Australia in the Paleocene (Stover & Partridge, 1973). It is rare in the pre-Miocene of Borneo. In the early Miocene there is a marked increase and it remains abundant thereafter (Muller, 1972), just as it does in southeast Australia. It is also present in the oldest Tertiary flora in Queensland.

TABLE 2. Pollen common to Borneo, Queensland, and SE Australia in the Tertiary. Key to the taxa shown in Fig. 16.

Botanical Affinity	Fossil Name(s)	References
1. *Ilex*	*Gemmatricolporites permagemmatus*	Muller, 1968
	Ilexpollenites spp.	Martin, 1977b; Hekel, 1972
2. Myrtaceae	*Myrtaceidites* spp.	Muller, 1968; Stover & Partridge, 1973; Hekel, 1972
3. *Anacolosa*	*Anacolosidites* spp.	Germeraad et al. 1968; Stover & Partridge, 1973; Hekel, 1972; Harris, 1965b.
4. Unknown	*Striatocolporites minor*	Muller, 1968; Hekel, 1972
5. Rhizophoraceae	*Zonocostites ramonae*	Germeraad et al., 1968; Hekel, 1972
6. *Nypa*	*Spinozonocolpites prominatus* = *S. echinatus*	Muller, 1968; Stover & Evans, 1973; Hekel, 1972
7. *Alchornea-Coelebogyne*	*Psilatricolporites operculatus*	Germeraad et al., 1968; Martin, 1974; Hekel, 1972
8. Compositae	*Echitricolporites spinosus* *Tubulifloridites antipodica*	Germeraad et al., 1968; Stover & Partridge, 1973; Hekel, 1972
9. *Austrobuxus* (= *Longetia*)-*Dissiliaria*	*Malvacipollis diversus*	Muller 1972; Stover & Partridge, 1973; Hekel, 1972

Anacolosa does not appear in northeast Queensland until the late Oligocene (Hekel, 1972), although it is present in the Paleocene Brisbane microfloras of southeast Queensland (Harris, 1965b). Other pollen types found in both Borneo and Queensland before the Miocene are shown also in Fig. 16 (Muller, 1968; Germeraad et al., 1968; Hekel, 1972) and include Rhizophoraceae, *Nypa*, *Alchornea*/*Coelebogyne*, and Compositae. In southeastern Australia in the early Eocene, at a time of low sea level, *Nypa* probably formed extensive mangrove forests on the exposed continental shelf, particularly in the Bass Strait between Tasmania and mainland Australia. A rapid rise in sea level subsequently inundated these forests (Partridge, 1976).

Mangrove pollen of the *Sonneratia* type and Rhizophoraceae become important in Borneo in the Oligocene. The ancestral type of *Sonneratia* may extend into the latest Eocene. *Nypa* and the *Brownlowia*-type pollen are the only mangroves present in the Eocene, perhaps suggesting that mangrove vegetation was not well developed then. In the late Miocene, other mangrove taxa become important. These include *Acanthus*, *Aegialites*, *Avicennia*, and *Camptostemon*. There is thus a history of the gradual appearance of the modern mangrove vegetation (Muller, 1964; Morley, 1977).

Pollen of Asiatic montane taxa become common and abundant in the Oligocene-early Miocene of Borneo. These taxa include *Pinus*, *Picea*, *Tsuga*, and *Alnus*. Some of these pollen types are notorious for long distance dispersal but their abundance indicates that they must have been growing locally. The montane pollen is found in assemblages with the tropical lowland mangrove pollen. Geological evidence indicates mountain building in the areas bordering the depositional basins, and that these mountains had been reduced by erosion by the late

Miocene when there was further uplift (Muller, 1966, 1972). Apart from these selected taxa, there are no other published accounts of Oligocene floras for southeast Asia.

A Miocene coal from Borneo has been studied in detail and compared with a Holocene peat and the present-day swamp vegetation. There are some 76 spore and pollen types and the floristic composition of the coal and peat is closely comparable. Any minor differences can be attributed to ecologic variation, etc. Only one pteridophyte spore, *Stenochlaena areolaris*, has become extinct since the Miocene (Anderson & Muller, 1975) although it is present elsewhere in the Philippines today. Thus the flora takes on a modern aspect in the Miocene (Morley, 1977) and has remained much the same to the present day in this particular location. In the montane record, however, the austral taxa *Podocarpus* sect. *Dacrycarpus* and *Phyllocladus* appear in the late Pliocene-Pleistocene (Muller, 1966). In the Pliocene, pollen of Acanthaceae, Balsaminaceae, Compositae, Gramineae, and Loranthaceae increase in frequency and diversity (Morley, 1977). In the Quaternary, several lines of evidence indicate a more seasonal climate in the Sunda area (Morley, 1977) but the palynological record is very meager for this period.

In New Guinea, pollen floras from the Central Delta region of Papua extend back to the late Miocene and consist mostly of contemporaneous taxa. Spores of pteridophytes generally dominate the counts. Gymnosperms are present in very low frequencies and include *Microcachrys* and/or *Microstrobus* (which disappeared in the late Tertiary), *Podocarpus* section *Dacrycarpus* and other *Podocarpus* spp., *Dacrydium*, Araucariaceae, and probably the cycad-type. Of the angiosperm pollen, the mangroves Rhizophoraceae and Sonneratiaceae are the most abundant together with Palmae. *Nothofagus*, the *brassii* pollen type (now growing in the New Guinea highlands) is present but usually 10% or less of the total pollen counts, suggesting that it was probably transported into the area of deposition. There are a few grains of the *fusca* type of *Nothofagus* and it is uncertain whether this represents long distance dispersal or a rare presence in New Guinea. Small quantities of Rubiaceae, Proteaceae, Casuarinaceae, Myrtaceae, and Malvaceae are present (Khan, 1974). This region of New Guinea has always been part of the Australian plate. The oldest record, however, dates from a time when the southeast Asian and Australian plates were in contact. The pollen flora largely reflects the deltaic environment of deposition with some pollen being transported in from the surrounding regions.

DISCUSSION

The Australian paleobotanical record shows major changes in the mid-late Eocene, the Miocene, and the end of the Pliocene. These changes coincide broadly with major declines in the oxygen isotope temperature curve (Fig. 4). The mid-late Eocene changes are associated with the opening of the seaway south of Australia. The Miocene change is associated with the Antarctic ice-cap reaching major proportions and developing aridity in Australia. The changes at the end of the Pliocene are associated with the onset of the glacial cycles and aridity in Australia reaching its present dimensions. These changes are shown clearly in

the abundant pollen groups shown in Fig. 9, but many of the low frequency pollen types show changes about the same time.

The Tertiary pollen assemblages show general and distinctive patterns for any one geological age. Some changes in the Australian flora through the Tertiary may be postulated thus:

Early Paleocene: Gymnosperms are probably the major element and angiosperms are still increasing in importance. There are many extinct taxa.

Late Paleocene–Eocene: 'Proteaceae' are more abundant and very diverse. This abundance is surprising, given the low pollen production of this taxon today (Martin, 1978). If these Tertiary 'Proteaceae' were trees, then more pollen would be produced when compared with a sclerophyllous shrub layer, especially if the trees were those of the high canopy (Birks & Birks, 1980). Some proteaceous trees are found in Queensland rainforests today, but pollen counts are low (Kershaw, 1970b). It is possible that these ancient 'Proteaceae' were one of the dominants in the vegetation. Many of the taxa are extinct.

Late Eocene, Oligocene, and Early Miocene: Nothofagus is the dominant pollen type in the pollen assemblages but, given its heavy pollen production, it may not have been the dominant in the vegetation, although more abundant than formerly. Other low pollen producers that are usually present in the assemblages may have been just as abundant in the vegetation.

Miocene and Pliocene: Myrtaceae becomes the dominant. The eucalypt pollen type (which may include other genera) is present but not abundant, except perhaps in southwestern Australia (Bint, 1981), assuming reliable identification of *Eucalyptus*.

Late Pliocene and Early Pleistocene: The present floristic zones and vegetation probably became established about this time, but this assumption is based on the climatic evolution, for the fossil record is too scanty to support it. Besides these overall trends, there are shorter fluctuations in the pollen record (see Figs. 11, 12), which are probably the result of climatic fluctuations, but the 'resolution' of dating is not sufficient to allow any correlation with a causal factor such as the oxygen isotope curve or sea level changes.

Most of the variation seen in the Tertiary assemblages is consistent with the hypothesis that there was a Tertiary climatic gradient parallel to that seen today, i.e. drier inland and wetter on the coast, particularly in the southeast corner of Australia. (The inland region was, however, relatively well watered through most of the Tertiary when compared with its present state.) Myrtaceae becomes abundant first in inland New South Wales and later in southeast Victoria, whereas *Nothofagus* declines first in Queensland, then inland Australia, and last in southeast Victoria, where small remnant stands of *Nothofagus cunninghamii* are still present today. The development of open woodland and/or savannah started first in Central Australia, then possibly in the north, and finally in southeast Australia. Some present-day patterns appear to be fore-shadowed even in the early Tertiary, following the climatic gradient. *Dacrydium franklinii* was more abundant in southeastern Victoria, during the late Eocene early Oligocene, close to its present distribution in Tasmania. Not all taxa fall into this category. *Ilex* found today across the north of Australia does not extend south of latitude 18°10′S in Queens-

land yet it is present in the early Tertiary in southeast Australia when it was adjacent to Antarctica.

There are general similarities between the Australian and New Zealand paleobotanical record, even though these two land masses have remained at approximately the same distance of 2,000 km from each other throughout the Tertiary. The increase in abundance of *Nothofagus* in the Eocene is seen in both. New Zealand was as much affected by the opening of the seaway around Antarctica as was Australia, so these similarities are not surprising. The Miocene was also a time of major change in New Zealand, for it too was influenced by the ice cap development on Antarctica. However, the Miocene marks a divergence, New Zealand being subjected to heavy glaciation that probably started in the Pliocene whereas Australia suffered increased aridity. This difference probably results from New Zealand remaining at the same latitude whereas Australia continued on its path northwards, although a small, insular landmass such as New Zealand is not strictly comparable to a continental landmass. This floral similarity is illustrated by the extinct Tertiary angiosperm taxa in New Zealand. Of the 200 or so extinct taxa in the palynological record, 70% occur in the Australian record also. About 20% are restricted to New Zealand, mostly in the Miocene (Mildenhall, 1980).

The early Tertiary floras of southeast Asia and Australia are quite different although the evidence from northern Australia, the most relevant region in this context, is very scanty. This difference is to be expected for two reasons: the different floristic inheritance and the different climatic zones that must have existed with a latitudinal distance of 3,000 km between the two continents. There are, however, a few taxa in common with both continents, even with southeast Australia. The most notable common taxon is the Myrtaceae, which appears first in Borneo, before Australia. There are more taxa in common, from Miocene time when the two continents came into collision, but there remain many differences which may be attributed to environmental differences.

Today the dry monsoonal climate and infertile soils of northern Australia are very limited in New Guinea, whereas the habitats for the complex lowland humid rainforests of New Guinea are restricted to a "small archipelago" of habitats on the Australian mainland (Webb & Tracy, 1972). Areas of seasonal drought and dry pockets are very restricted in the island archipelago of southeast Asia (see van Steenis, 1979, p. 107). This environmental difference is largely the result of different geological evolution, more active tectonism in New Guinea and elsewhere than on the Australian mainland. It is likely that this difference extended back into the Tertiary. With one published account for New Guinea and two for Queensland, the fossil record is too inadequate for further comparisons.

The increase in Myrtaceae in Borneo in the early Miocene, about the same time as it started increasing in Australia, is most interesting. The increase in Australia may be attributed to developing aridity, although independent evidence for the timing of this event is uncertain. However, it is unlikely that aridity was the cause of the increase in Borneo. In the vegetation of Borneo, Myrtaceae may be abundant on the infertile soils (J. Muller, pers. comm.). Although not studied in detail, Specht and Womersley (1979) described "heathlands" in Malesia. 'Heath forests' are considered as an edaphic climax rainforest developed on very infertile

soils. With increasing site severity the forest is replaced by open scrubland. Species of *Baeckea, Leptospermum, Eugenia, Tristania, Rhodamnia, Rhodomyrtus,* and *Xanthostemon* of the Myrtaceae are involved. A diagram of the heath-forests and scrublands in Bako National Park, Sarawak, shows Tertiary Sandstone as the parent rock (Specht & Womersley, 1979). Thus the increase in Myrtaceae in Borneo may be related to newly available infertile soils.

The hypothesis above, which accounts for the increase in Myrtaceae in Borneo, also questions the developing aridity as the cause of the increase in Australia. As discussed previously, there is evidence, such as quartz sands and gravels in the lower sediments in western New South Wales, that the soils may have been less fertile than those of today. *Nothofagus* and other rainforest taxa would have had to exist on these infertile soils as well as the Myrtaceae. However, some sites, such as narrow gullies, favor nutrient accumulation. In any given topography, a mosaic of soil fertility and available moisture would exist, even with a uniform parent rock material and climate (respectively). Consequently the different components of the pollen assemblage may not have been growing together, but the palynological method would not detect this. As discussed previously, adaptations to a low nutrient status lowers the growth rate, which appears to confer added drought resistance as well. Now, any taxon with a slower growth rate is at a serious competitive disadvantage if the climate is suitable for faster growing species. It is likely that the long history of infertile soils allowed the evolution of mechanisms of coping with infertility. Such taxa would be relegated to the most unfavorable sites while the climate was suitable for faster growing species, for some kinds of rainforest are capable of growing on relatively infertile soils, provided that rainfall is adequate (Webb, 1978). Once the climate started to become drier, the taxa on the unfavorable sites expanded their area. This expansion of Myrtaceae starts earlier in the west of western New South Wales, thus paralleling the climatic gradient. Independent evidence from the sediments, viz., that the carbonaceous content decreases about the time of the Myrtaceae increase, is interpreted as a decrease in swamp vegetation that would follow a drier climate. Most of the early Miocene Myrtaceae are not the *Eucalyptus* type. The whole assemblage indicates closed forest, even into the Pliocene and there is no known analogue in Australia for these myrtaceous forests. It is a matter for conjecture whether these Miocene-Pliocene myrtaceous closed forests were akin to the "heath forests" of Borneo today.

So far this paper has dealt with the barriers of water, topography, climate, soils, and distance. Reconstruction of the barriers of vegetation are more difficult because the palynological method is not suited for the detection of vegetation that may exist as a mosaic. Identifications are rarely to specific level and the ecological tolerances of a genus may encompass more than one vegetation type. It is possible to reconstruct the vegetation mosaic from the pollen assemblage, given incompatible ecological tolerances, but not with any great precision. *Acacia* in New Zealand provides a good example. In the early Miocene, *Acacia* is found on the eastern coast of the South Island in assemblages with abundant *brassii* pollen of *Nothofagus*. The whole assemblage indicates rainforests. *Acacia* is usually found in open vegetation, so it may have existed in exposed coastal situations subject to wind desiccation (Pocknall, 1981). However, there are a few

species of *Acacia* that are found in certain rainforests today (Webb & Tracy, 1981b) so this Miocene *Acacia* in New Zealand may have been a rainforest species also. *Acacia* appears in the Pliocene on the west coast of the North Island of New Zealand and becomes extinct during the Pleistocene (Mildenhall, 1975). The pollen assemblages in which it is found indicate coastal swamp sedges together with scrub and grassland species. Tree pollen is relatively rare and trees may have been restricted to the surrounding hills. Thus this second occurrence of *Acacia* in New Zealand is more in agreement with the ecological requirements of most Australian species today. Obviously, interpretations of pollen assemblages rely on a knowledge of the pollen behavior of the present vegetation. In a southeastern Australian study of some surface samples from small pockets of rainforest in vast areas of eucalypts, the rainforest was hardly detectable, quantitatively. (This study has important implications, viz., that very small areas of a different kind of vegetation that are biologically very important, may be almost undetectable by the quantitative palynological method.) Moreover, *Acacia,* regarded as one of the dominants in the *Eucalyptus* vegetation, was not recorded in the surface samples (Ladd, 1979). *Acacia* is a low pollen producer with very limited dispersal and it is never found in any quantity. These are examples of the problems of interpretation of pollen assemblages, particularly those of Tertiary age for which the present vegetation is not a good analogue.

Long distance dispersal is a controversial subject, but experience with the paleobotanical record leads to the conclusion that it has occurred. The best illustration of this is the similarity of the Australian and New Zealand Tertiary record. It is not known how this was accomplished, for much of the knowledge gleaned from present day observations of dispersal seems inapplicable to the fossil record. The reason for this probably lies in the vast geological time where the million-to-one chance has probably occurred many times. There are, however, mechanisms that make long distance dispersal possible. Birds transport seeds either in the gut or stuck to feet and feathers (Carlquist, 1981). Some birds migrate regularly. Birds may travel long distances in relatively short times. An example may be seen in opportunistic waterfowl, which rapidly move into flooded areas in inland Australia. Flooding may occur anywhere in the arid region after exceptional rains. When the floodwaters dry up, the birds disperse to the coast (Braithwaite, 1975) or as far away as New Zealand, Christmas Island or MacQuarie Island (G. van Tets, pers. comm.). The second mechanism is wind. Raven (1973) quotes a number of direct measurements of transport by the prevailing westerly winds of pollen, dust, smoke, and possibly pathogens from Australia to New Zealand. The prevailing westerlies probably could transport small seeds but would be unlikely to carry larger seeds. However, birds also use winds and some (e.g. albatross) regularly circle the globe in these latitudes. In New Zealand, the more recently arrived land birds are almost exclusively Australian (McDowall, 1969). Tropical cyclones produce winds that are much stronger than those of the westerlies. Tracks of the cyclones in the Australian region generally travel across the north, down the west coast and down the east coast, some of the latter eventually end up in New Zealand (Coleman, 1972). New Caledonia is well within the cyclone area. Tropical cyclones cause a great deal of damage and create the disturbance that may allow new introductions to become established. They also

carry birds off course. There are plovers in Tasmania and New Zealand, and it had long been assumed that they were the same. However, a more critical examination of the New Zealand plover showed its affinities with a Queensland form. It is thought that tropical cyclones assisted the plovers in their journey to New Zealand (G. van Tets, pers. comm.). It is not intended to pursue this topic further, but simply to establish the following points: (1) The paleobotanical record indicates long distance dispersal has occurred; (2) mechanisms exist for long distance dispersal; and (3) the vast geological time where the most unlikely of probabilities may have occurred a number of times. In any case, dispersal does not succeed unless the environment at the end of the journey is suitable for growth and establishment. It appears that the environment of New Zealand and Australia was sufficiently similar to allow long distance dispersal to succeed.

Conclusions

Throughout this study, climate emerges as the most important environmental factor, for changes in the paleobotanical and paleoclimatic records usually go together. It is doubtful whether climate has acted as a barrier within Australia, through most of the Cenozoic. The arid center, a conspicuous barrier today, only reached full development in the late Tertiary, some 2.5 million years ago. Through most of the Tertiary, habitats suitable for closed forest existed in central Australia, though not necessarily continuous. Although the center was relatively well watered, there is evidence of a Cenozoic climatic gradient parallel to that of today, i.e. drier in the center and wetter on the coast. Such a gradient would provide a diversity of habitats. There may have been a north-south temperature gradient during the Tertiary, judging from the greater abundance of *Nothofagus* in southeastern Australia when compared to Queensland, but there is no independent evidence to support this.

Climate appears to have been no great barrier between Australia and New Zealand. Both of these land masses have been in the same latitudinal zone through most of the Tertiary and subjected to the same major influences on climate, viz., proximity to and ice cap development on Antarctica. The paleobotanical record is generally similar through most of the Tertiary, becoming less similar in the Pliocene when glaciation becomes increasingly important in New Zealand. The difference in climate between Australia and Southeast Asia must have been a barrier, as would be expected from a latitudinal distance of 3,000 km in the early Tertiary. The paleobotanical records are quite different as well. There is evidence of very limited migrations after these two land masses came into collision in the Miocene, for the seasonally dry habitats, so widespread in Australia, are very restricted in Southeast Asia. As well, such seasonal habitats may have had a relatively late development.

Soil fertility has probably played an important role, in conjunction with climate. Although documentation of Cenozoic changes in fertility is sparse, the limited evidence suggests that, during the Tertiary, some soils were even less fertile than those of today. Adaptations to low fertility through a slower growth rate may enhance drought resistance. Hence some of the Tertiary flora may have possessed adaptations before the development of aridity. Low fertility soils are widespread in Australia but probably not so common in Southeast Asia. The

increase in Myrtaceae in both Australia and Borneo is thought to be due to a combination of low fertility soils and perhaps developing aridity in Australia, but to newly available infertile soils in Borneo. That these two events both occur in the Miocene is probably only a coincidence.

The major topographic features in Australia have remained more or less the same through most of the Cenozoic. Tectonics have been very minor and gentle. Rather than acting as barriers, these factors have probably been important in maintaining habitat diversity. Tectonism has been more active in Southeast Asia, and topographic differences much greater, so these two factors may have been greater barriers to migration between Australia and Southeast Asia after these two plates came into collision.

Continental drift has had a major influence on the evolution of climate and this has been its most important effect within Australia throughout the Cenozoic. New Zealand has remained at approximately 2,000 km from Australia for the whole of the Cenozoic, but this distance appears to have had little effect as a barrier. The 3,000 km between Southeast Asia during the early Tertiary appears to be a barrier, which, however, may have been more of climate than of distance. After these two plates came into collision, there has been only limited migration, for the barriers of climate and soils remained and are seen today.

Barriers and migrations are concepts derived from historical biogeography, which is essentially the study of present day distributions. Historical biogeographers have traditionally held the hypothesis that a taxon originates somewhere (by evolution) and then spreads its range by dispersal, which may be stopped by barriers or channelled along migratory pathways. By closely studying some characteristics of the taxon and its distribution, they then work this hypothesis backwards to arrive at some explanation of how the present distributions came to be. The unstated assumption of this practice is: provided all other factors remain equal and stable. This study shows clearly that all other factors are not equal or stable, but that there is a complex, interwoven and continuously changing environment and flora. Although I have attempted to use the concepts of barriers and migrations, they seem inappropriate in this study, which essentially follows paleoecological principles.

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WALLACE'S LINE: A RESULT OF PLATE TECTONICS[1]

T. C. WHITMORE[2]

Wallace's line is one of the sharpest and first detected zoogeographical boundaries on earth. This line, running north to south through the center of the Malay archipelago, separates predominantly Asian faunas to its west from predominantly Australasian faunas to its east. The sharpness of the boundary differs from group to group, dependent on the dispersibility of the group under consideration. For rain forest plants Wallace's line is a less marked boundary. To its west Australasian plants occur mainly on oligotrophic podzolized sands in heath forest. Asian plants massively penetrate to its east and the Australasian element is perhaps most predominant in certain mid-mountain forests rich in *Nothofagus* or the conifers *Agathis* and *Araucaria*.

Malesia has an extremely rich flora, conservatively estimated to comprise 25,000 species of flowering plants (van Steenis, 1971) and this has contributed to the view that the 'cradle of the angiosperms' lies somewhere between Assam and Fiji (Takhtajan, 1969; Smith, 1970).

Until recently different viewpoints on the palaeogeography and biogeography of the Malay archipelago had to stand or fall on their ability to fit all known facts into a plausible hypothesis. There was no external point of reference. Biologists tended to make geographical reconstructions and geographers to use biological evidence.

The revolution in the earth sciences during the last two decades, which has resulted from the theory of plate tectonics, means that the palaeogeography of the globe during the Mesozoic and Cenozoic is now understood in general terms. Now biologists can for the first time work with a broadly painted background of established palaeogeographical facts, albeit still lacking much fine detail, rather than mere suppositions. The former dangers of circular argument, which have so often plagued discussions of biogeography, no longer befog the scene.

The major events of global geology that affect the biogeography of the region of Wallace's line are the progressive break up of Gondwanaland from about 140 m.y.a. (Jurassic/Cretaceous boundary) and the drifting north of the Indian fragment to collide with Laurasia at about 55 m.y.a. and of the Australia/New Guinea fragment to collide with the southeastern extremity of Laurasia at only about 15 m.y.a., the mid-Miocene. Before that the Malay archipelago did not exist.

Plants and animals could have reached modern Malesia from one of three sources, Laurasia, Gondwanaland via Australia, or Gondwanaland via India followed by southeastwards migration.

Before we look at some present-day phytogeographic patterns and see how

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[1] This paper distils some of the highlights from a recent book 'Wallace's Line and Plate Tectonics' (Whitmore, 1981). It was presented at the symposium Plant Geographical Results of Changing Cenozoic Barriers at the XIII International Botanical Congress, Sydney, Australia, 1981.

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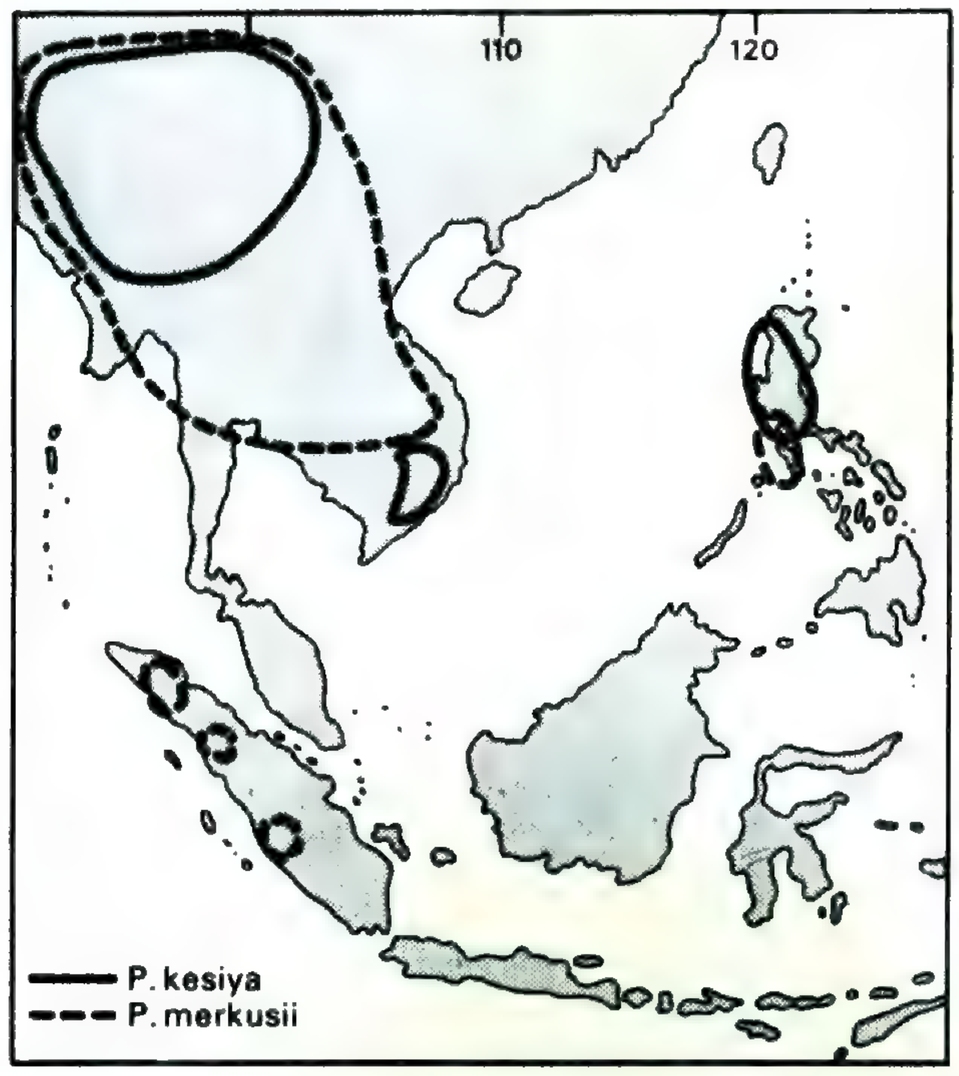

FIGURE 1. *Pinus* in Malesia. Reproduced from Whitmore, 1981, fig. 8.1.

they reflect this history we must first consider palaeoclimate. Both animals and plants are variously confined to particular habitats. Contemporary distributions are likely partly to reflect past differences in climate. The interpretation of range must penetrate this veil and take it as well as palaeogeographic dispositions of land into account.

It is now known that there have been major fluctuations in tropical climates. During ice ages sea-level was lowered by up to 180 m, rainfall was less and areas with a seasonally dry climate more extensive. In Africa and tropical America there was substantial desiccation. Rain forest was restricted to pockets, so-called refugia, set like islands in a 'sea' of seasonal forest and savanna. The rain forest patches were to some extent in contact through gallery forests along rivers. Today tropical rain forests are at or near their greatest extent, achieved for only a small fraction of the last two million years. In Africa and America centers of species richness and endemism have been detected within the rain forest and these are believed to represent the refugia.

The Malesian rain forest occurs in two great blocks. The western or Sunda shelf block is centered on Sumatra, Malaya, and Borneo. The eastern, Papuasian or Sahul shelf, block is centered on New Guinea. Between the blocks lies a north-south belt of seasonal forests running through the western Philippines and Celebes to the Lesser Sunda Islands. The whole of each block is of comparable species richness and endemism to one of the rain forest refuges of Africa or America. There is as yet no geoscientific (geomorphological or pedological) or palynological evidence of more extensive seasonal climates in Malesia. Nevertheless these two blocks are likely to have been of reduced extent at the ice age maxima. We may speculate that seasonal forests developed mainly on land exposed by low sea level and which is now flooded, e.g. as the South China Sea (beneath which indeed true laterite and kunkur nodules are evidence of subaerial exposure and seasonality). There would probably also have been extensive forests under the

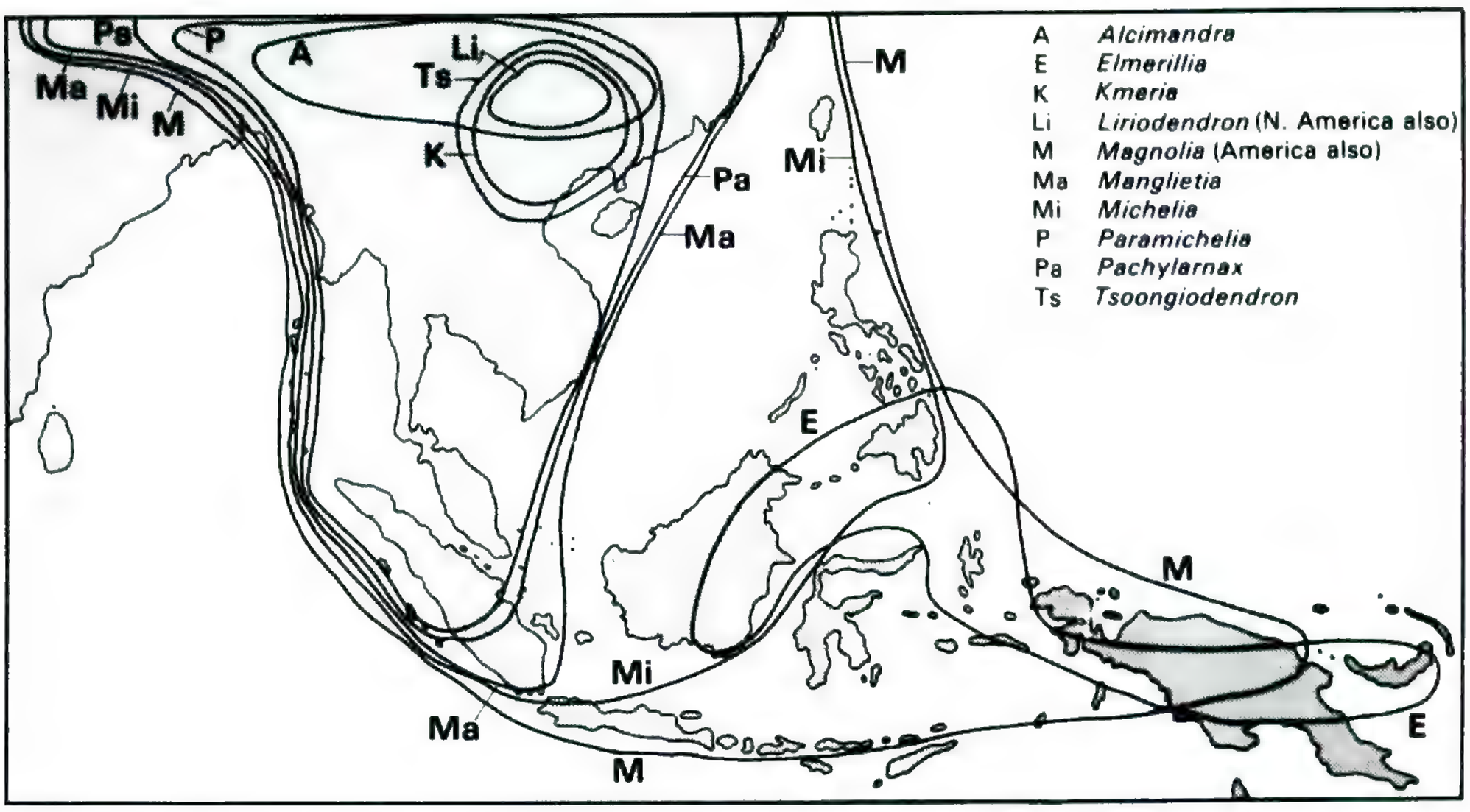

FIGURE 2. The ranges of the genera of Magnoliaceae in Malesia and southeast Asia. Reproduced from Whitmore, 1981, fig. 8.4.

influence of saline water on the low, exposed land (i.e. mangrove and brackish water swamp forests).

Thus, we may conclude that most of the present-day areas of rain forest have been continuously forested. Do the ranges of rain forest plants therefore reflect the palaeogeographical history?

LAURASIAN GROUPS

It is well established that the Coniferae divide into two great classes of northern and southern hemisphere range respectively (Florin, 1962). Both classes have representatives in Malesia. Amongst the northern conifers only *Pinus* (Fig. 1) extends into Malesia at the present day. It is represented by two species, *P. kesiya* and *P. merkusii*, of partly overlapping ranges. For both, the Malesian stations are the extremity of a wide range in seasonally dry continental southeast Asia.

Six genera of Magnoliaceae occur in Malesia and four more are endemic to the region of southern China and northern Indo-China (Fig. 2). Within Malesia *Elmerrillia* is endemic from eastern Borneo to New Britain. There is a very marked concentration in western Malesia. Magnoliaceae as a family are strongly concentrated in subtropical east Asia and extend into Malesia from this bastion becoming progressively less well represented eastwards. Magnoliaceae are accepted by most botanists to be a primitive family. The distribution contrasts strongly with that of Winteraceae, also regarded as primitive, which is described below.

PAPUASIAN GROUPS

Phyllocladus, the 'Celery Pine' is a small genus of the big southern conifer family Podocarpaceae. There are three species in New Zealand, one in Tasmania,

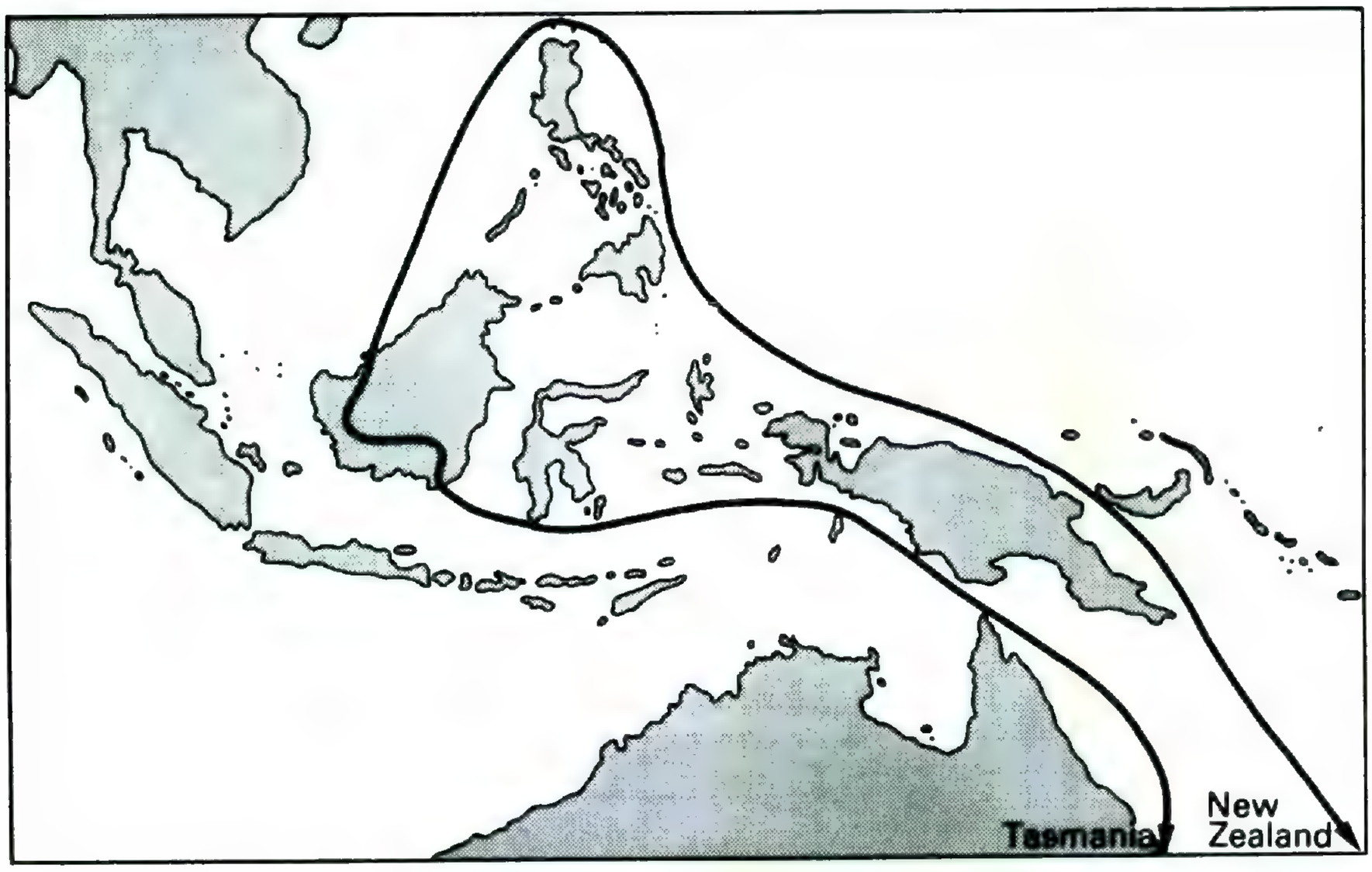

FIGURE 3. The range of *Phyllocladus*, Podocarpaceae. Reproduced from Whitmore, 1981, fig. 8.6.

and one, *P. hypophyllus*, in montane rain forests in Malesia extending west as far as Philippines and eastern Borneo (Fig. 3). The range is strongly Gondwanic. It is of interest that in pollen profiles from northern Borneo, which extend from the Oligocene (30 m.y.a.) onwards, *Phyllocladus* pollen suddenly appears at the Plio-Pleistocene boundary, 2–3 m.y.a. (Muller, 1966). *Podocarpus imbricatus* pollen appears at about the same time.

The primitive family Winteraceae is strongly centered on the islands of the southwest Pacific (Fig. 4; Smith, 1943; Vink, 1970). There are three genera in eastern New Guinea, of which *Drimys* extends westwards to cross Wallace's line into the Philippines and eastern Borneo. Winteraceae is the southern counterpart of Magnoliaceae.

MALESIAN GROUPS OF APPARENTLY DUAL ORIGIN

There is not much doubt that the families so far considered entered Malesia from either Laurasia or Gondwanaland. Any alternative hypothesis would offend Occam's razor. It is more difficult to identify families that have arrived from both directions as this presupposes a very thorough understanding of the group in question.

Proteaceae have been the subject of very detailed investigation (Sleumer, 1955; Johnson & Briggs, 1975). The family is concentrated in the southern hemisphere and strongly concentrated on Australia and the southern tip of Africa. The ranges of seven Australian genera extend into Malesia (Fig. 5) and one genus, *Finschia*, is endemic to east Malesia and the southwest Pacific. However, the genus *Heliciopsis* presents an anomaly. This is endemic to Malesia and adjacent Asia. Johnson and Briggs believed that *Heliciopsis* could have reached southeast Asia from West Gondwanaland by the 'Noah's Ark' medium of India in which it subsequently died out. Proteaceous pollen has been found in the Eocene of India.

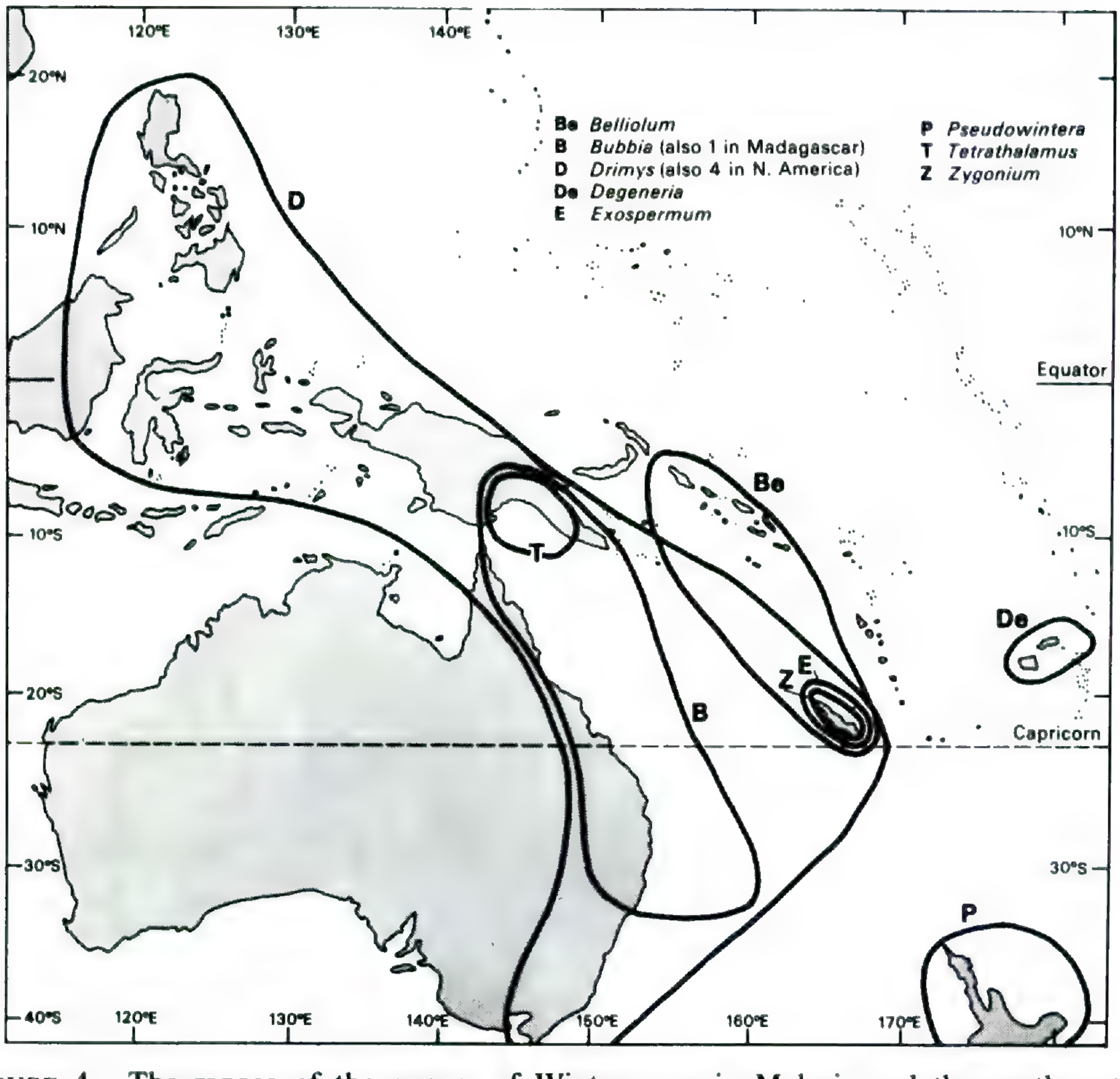

FIGURE 4. The ranges of the genera of Winteraceae in Malesia and the southwest Pacific. Reproduced from Whitmore, 1981, fig. 8.9.

Nastus, a small genus of ca. 15 species of bamboos that scramble through the canopy of tropical forests, occurs in Java, Sumba and Flores, and possibly Sumatra. It is also in New Guinea, the Bismarcks, and Solomons. *Nastus* also occurs on the south India Ocean islands of Réunion and Madagascar (S. Soenarko—Dransfield, pers. comm.). This range suggests a West Gondwanic origin followed by arrival in Malesia via both Laurasia and Australia/New Guinea. *Livistona* is a genus of fan palms of the rather primitive Coryphoid group. It is strongly represented at the western and eastern extremities of Malesia with few species in the center (Fig. 6). There is a series of species of great morphological diversity and relict distribution in Australia and a scarcely distinct related genus (*Wissmannia*) in the Horn of Africa. The picture may represent a relic of a much wider distribution that could have come from a west Gondwanic origin arriving in Malesia from both ends (Dransfield, 1981).

THE REMAINING ENIGMA

Fagaceae instance one of the great remaining puzzles of phytogeography. Subfamily Fagoideae have two genera. The true beech *Fagus* has a northern hemisphere range extending to southern China. The other genus, *Nothofagus*, the southern beech, reaches northwards from Australia and New Zealand to

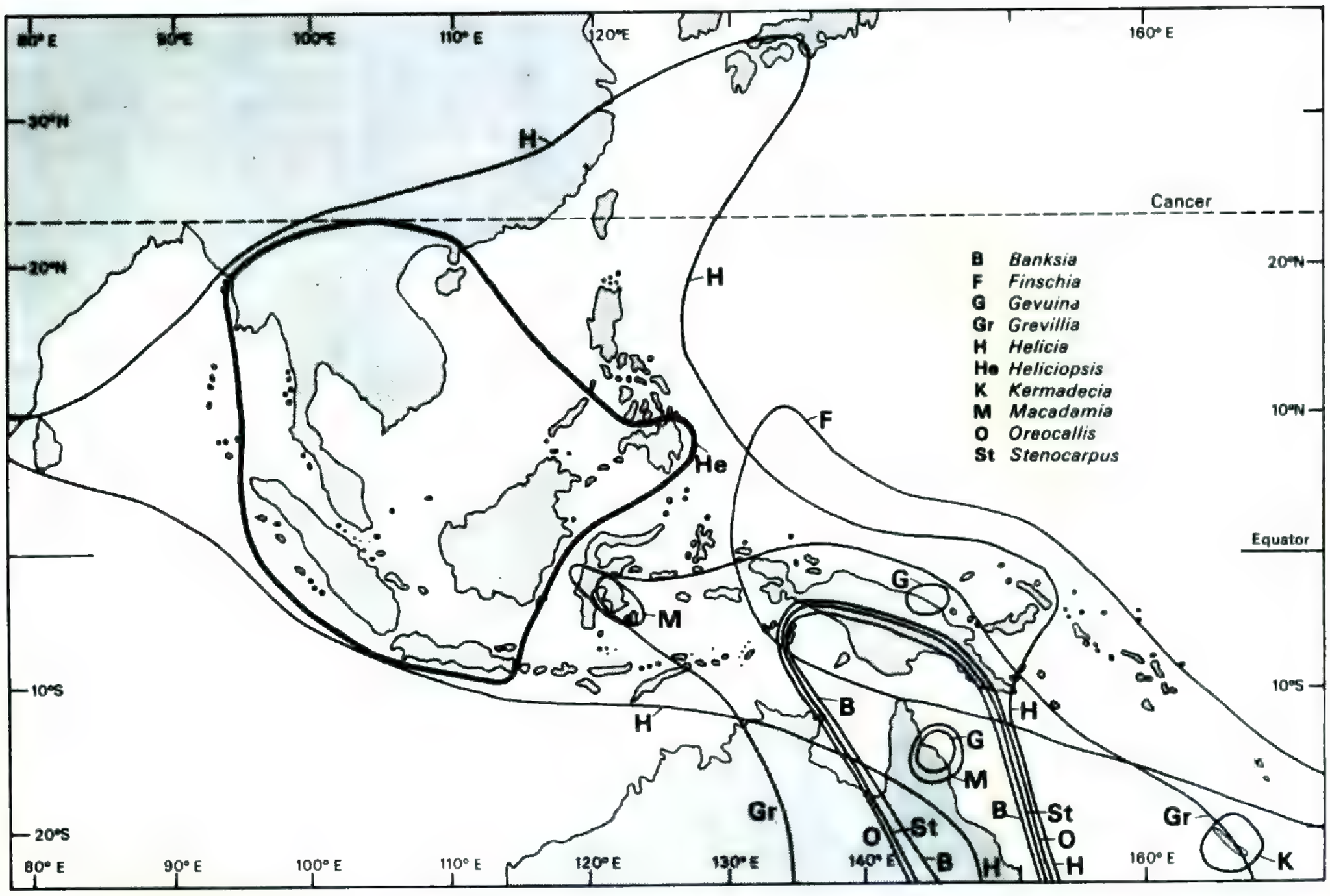

FIGURE 5. The ranges of the genera of Proteaceae in Malesia and southeast Asia. Reproduced from Whitmore, 1981, fig. 8.11.

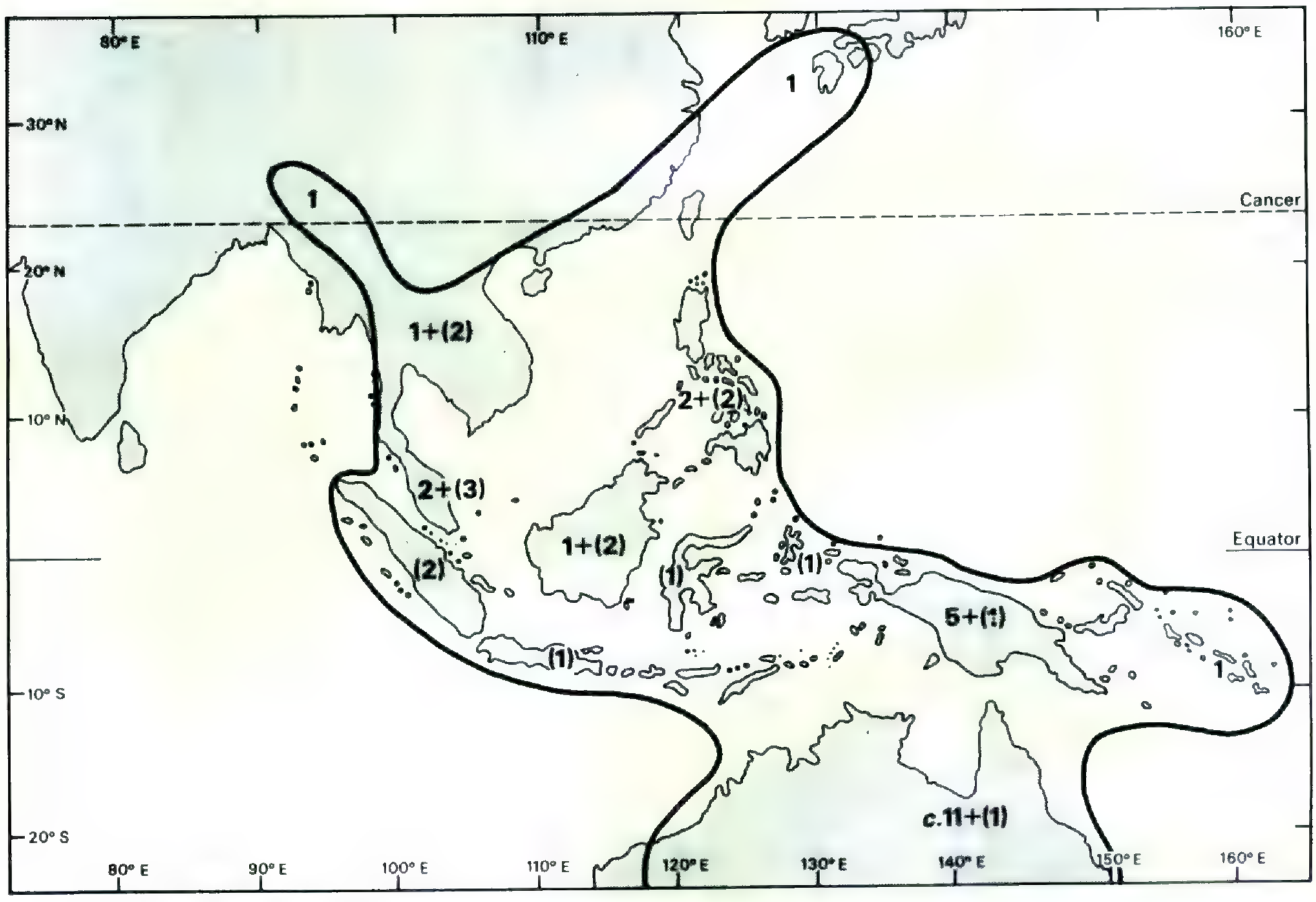

FIGURE 6. The distribution of the species of *Livistona*. Numbers of endemic and, in parentheses, non-endemic species shown. Reproduced from Dransfield, 1981, fig. 6.9.

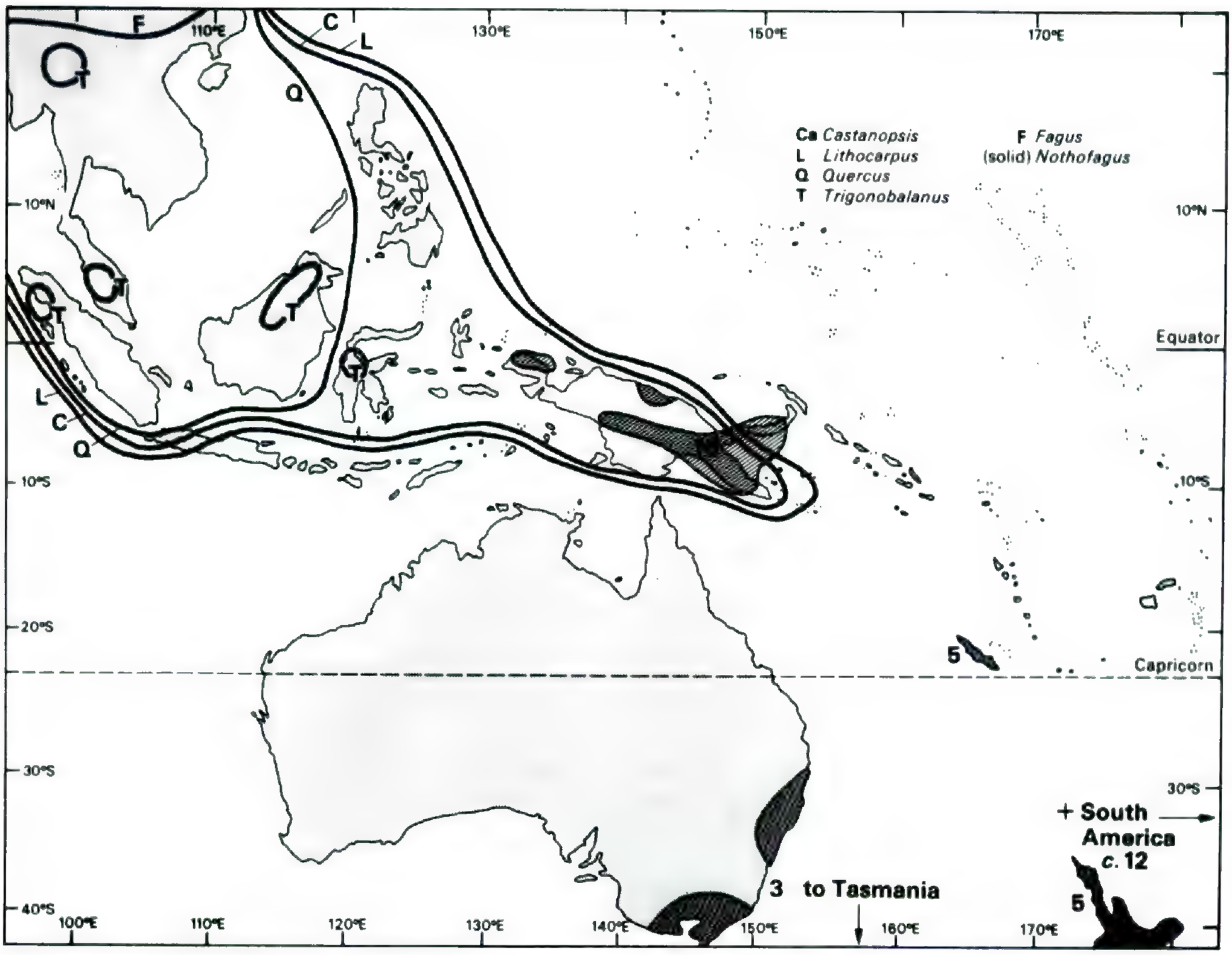

FIGURE 7. The ranges of the genera of Fagaceae in southeast Asia, Malesia, and the southwest Pacific. Reproduced from Whitmore, 1981, fig. 8.13.

eastern New Guinea (Fig. 7). The region of Southeast Asia and Malesia is where the ranges of the two genera of this undoubtedly natural subfamily came closest together. Magnoliaceae of the northern hemisphere and Winteraceae of the southern hemisphere are both families widely believed to be primitive and related. Their ranges overlap only in Malesia. Other pairs of northern and southern families that similarly overlap are Ericaceae and Epacridaceae (*Styphelia*), Staphyleaceae and Cunoniaceae, and Saxifragaceae and Escalloniaceae.

Botanists have attempted to account for these bihemispheric pairs, though controversy is likely to continue to rage in the absence of either a fossil record or an accepted view of evolutionary relationships within the group under discussion. Many angiosperm families appear to have originated in western Gondwanaland and moved out simultaneously with the break up of that great southern continent (Raven & Axelrod, 1974).

Malesia is the region where these groups come closest at the present day. In some cases their ranges overlap. What is known of evolutionary rates and the evidence of micro and macro fossils (Muller, 1974) makes it improbable that these pairs could have evolved in the last 15 million years or that they could have evolved on either the Laurasian or Gondwanan margin and spread throughout the globe since the collision. This enigma was recently pinpointed by van Steenis (1979), who postulated there must have been contact between north and south

long before the mid-Miocene collision. Close examination of the geological record shows that there is the possibility of an earlier connection and this has recently been explored by Audley-Charles et al. (1981). About late Jurassic or early Cretaceous the northwest continental margin of Australia was block faulted. The continental block that is believed to have separated from the Australian continent has not been identified. It could perhaps have been subducted at the Java trench or its ancestor. Alternatively it could be extant and lying somewhere northeast of present-day India, for at the time of its separation from Australia northwest Australia lay close to northeast India. Very recently Mitchell (1981) has identified south Tibet and Burma-Thailand as former parts of Gondwanaland that were rifted away from that continent in the later Permian or early Mesozoic (ca. 200 m.y.a.). However, the evidence for dating the separation is sufficiently uncertain to allow them to be considered tentatively as the missing fragment of northwest Australia.

This interpretation must at present be tentative. It rests on two areas of uncertainty. We need to know more, firstly, on the date of drift of Mitchell's continental fragment. Secondly, we have as yet inadequate knowledge on the timing and course of evolution of flowering plants. Fossils are sparse.

In conclusion, despite the revolution in the earth sciences of the last two decades, which has led to a total reappraisal of the biogeography of the Malay archipelago, Wallace's Line remains today, as for the past 120 years, a cogent influence, powerfully able to generate hypotheses subject to further test. It is still a challenge to biogeographers and geologists.

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CAUSES OF SHORT-TERM SEQUENTIAL CHANGES IN FOSSIL PLANT ASSEMBLAGES: SOME CONSIDERATIONS BASED ON A MIOCENE FLORA OF THE NORTHWEST UNITED STATES[1]

AUREAL T. CROSS AND RALPH E. TAGGART[2]

ABSTRACT

Several geologic and edaphic factors as well as climate appear to exert control over types of fossil assemblages in successive stratigraphic sequences in the Miocene of eastern Oregon and western Idaho. Direct geological control of plant communities included volcanic activity (gaseous, pyroclastic, and liquid ejecta), which may have killed plants and disrupted communities by explosive force, noxious gases, and the burial or smothering effect of cinder and ash falls and mudflows (lahars). Indirect, longer-term effects are caused by tectonism in the immediate area (graben-horst shifts, regional uplift, basin development, etc.), and at a considerable distance (climatic modification, rain shadow, continentality). Fossil representation is also modified by transportability, distance of transport, and durability of plant matter; availability and permanence of favorable sites for preservation; the nature, rate, and continuity of sedimentation; and the extent of selective destruction of the vegetation. In the Succor Creek Formation, volcanism, tectonic activity, and fire have affected vegetation dynamics, resulting in the presence of successional communities that might otherwise be attributed to significant climatic change if stratigraphic control were lacking. Typically successional communities tend to develop toward stable forests unless or until disrupted by further disturbance. Intervals of non-deposition and/or erosion leave gaps of varying and unknown magnitudes in the stratigraphic sequences. The time represented by each of the several stratigraphic units is only a fraction of the total Succor Creek time (1–2 m.y.), probably a thousand to a few thousand years.

INTRODUCTION

The Succor Creek Flora is contained in a thick sequence of volcanic rocks along Succor Creek and the eastern part of the Owhyee River watershed in Malheur County of southeastern Oregon and Owyhee County of southwestern Idaho (Fig. 1). The area of the principal exposures is bounded on the west by the Owyhee River, on the east by the western end of the Snake River Plain, and exposures extend into and around the north end of the Owhyee Mountains on the south.

GEOLOGY

The rocks in the Owyhee area are a complexly interrelated series of basalt and rhyolite flows, rhyolitic ash-flow tuffs, air-fall volcaniclastics of ash and pumice, water-laid ash and lacustrine sediments ranging from a mixture of volcani-

[1] We acknowledge with our sincere thanks: Dr. Alan Graham, Dr. Arthur R. Green, Dr. Lawrence E. Kittleman, Dr. Charles L. Rosenfeld, and Dr. Helen V. Smith for discussions and other assistance and information relative to the geology and the fossil plant collecting sites and collections of the Succor Creek area; Dr. J. Platt Bradbury for examination of diatom-rich samples; Curators of the Michigan State University Beal-Darlington Herbarium, Dr. John H. Beaman and Dr. Susan R. Kephart; and Loretta S. Satchell, Kurtis C. Kelley, and Catherine Caswell for field and laboratory assistance.

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clastic sediments to lignite and diatomite. Kittleman et al. (1965) summarized the surface geology and general stratigraphy and described several formations of Miocene and Pliocene age, including the Sucker Creek Formation.[3] The Sucker Creek Formation consists of "altered tuffs and volcanic sandstones, vitric tuffs, arkose sandstone, granite-cobble conglomerates, and carbonaceous volcanic shales" (Kittleman et al., 1965, p. 6).

The Type section (Fig. 1, locality 4) is about 200 m thick and contains only volcaniclastic rock, lignitic shales, and diatomite. Exposures at the northern end of the area measure more than 600 m in thickness (Fig. 1, loc. 15). Warner (1977), on the basis of four deep test holes drilled north and northeast of the area shown on Fig. 1, in the western end of the Snake River Plain (Fig. 2), has postulated the thickness in this deep part of the basin at about 2,000 m, the wells having penetrated nearly 1,500 m of strata identified as Sucker Creek Formation.

Near locality 15, a tabular basaltic flow, the "Bishop's Ranch Basalt," is included in the formation. A rhyolitic ash-flow tuff (Leslie Gulch Ash-Flow Tuff Member), which is lenticular in nature and about 300 m thick, is included in the Sucker Creek Formation about 20 km west of the Type section (loc. 4, Fig. 1). Lignites and lignitic shales from 1–10 m thick, are found in several local areas including the Coal Mine Basin (loc. 12), Whiskey Creek (loc. 3), McBride Creek (our "Shortcut" section, loc. 2), Rockville (loc. 1), Type locality and Rocky Ford section (loc. 4, 4a), and the Devils Gate section (loc. 9). Some of the sedimentary rocks have a vitric component that is usually altered to a greater or lesser extent, usually to montmorillonite minerals. Either glass shards or pseudomorphs of glass, altered to zeolitic minerals such as clinoptilolite and heulandite, are found in many of the fluvial and lacustrine beds. Some arkosic rocks contain a more complex suite of minerals, including sanidine and andesine, with quartz, biotite, and muscovite; and Kittleman et al. (1965) suggest that these may have been derived by water transport from granitic rocks of the Idaho Batholith (Fig. 2). Our own paleotopographic reconstructions suggest that this is unlikely in our study area and it is possible that the granitic core of the Owyhee's may have served as a more local source area.

The Sucker Creek Formation lies unconformably on a thick sequence of late Oligocene–early Miocene volcanics that were greatly faulted, uplifted, and eroded prior to the onset of a mid-Miocene episode of volcanism about 15 to 16 m.y.b.p. The Columbia River Group of mid-Miocene basalts (Fig. 3) is in part equivalent in age to the Sucker Creek Formation. The Sucker Creek is overlain unconformably by various late Miocene volcanics, including the Idavada Volcanics of early Pliocene age (Malde & Powers, 1962) and interfingers at the margins with the Columbia River Basalts. These Miocene rocks are considerably deformed by north-trending folds and northwest-trending faults (Fig. 3 and McBirney, 1978), which developed during the later Miocene, Pliocene, and Pleistocene.

The age of the Sucker Creek Formation has not been clearly established. A

[3] The original name "Succor" is now generally used but the spelling "Sucker" has been more extensively used. Kittleman used "Sucker Creek" when describing the Formation, which therefore has priority. Sucker will be used here in reference to the stratigraphic sequence (and time) included in the Formation. However, we are following recommended use of "Succor Creek" to refer to geographic area, stream, and flora.

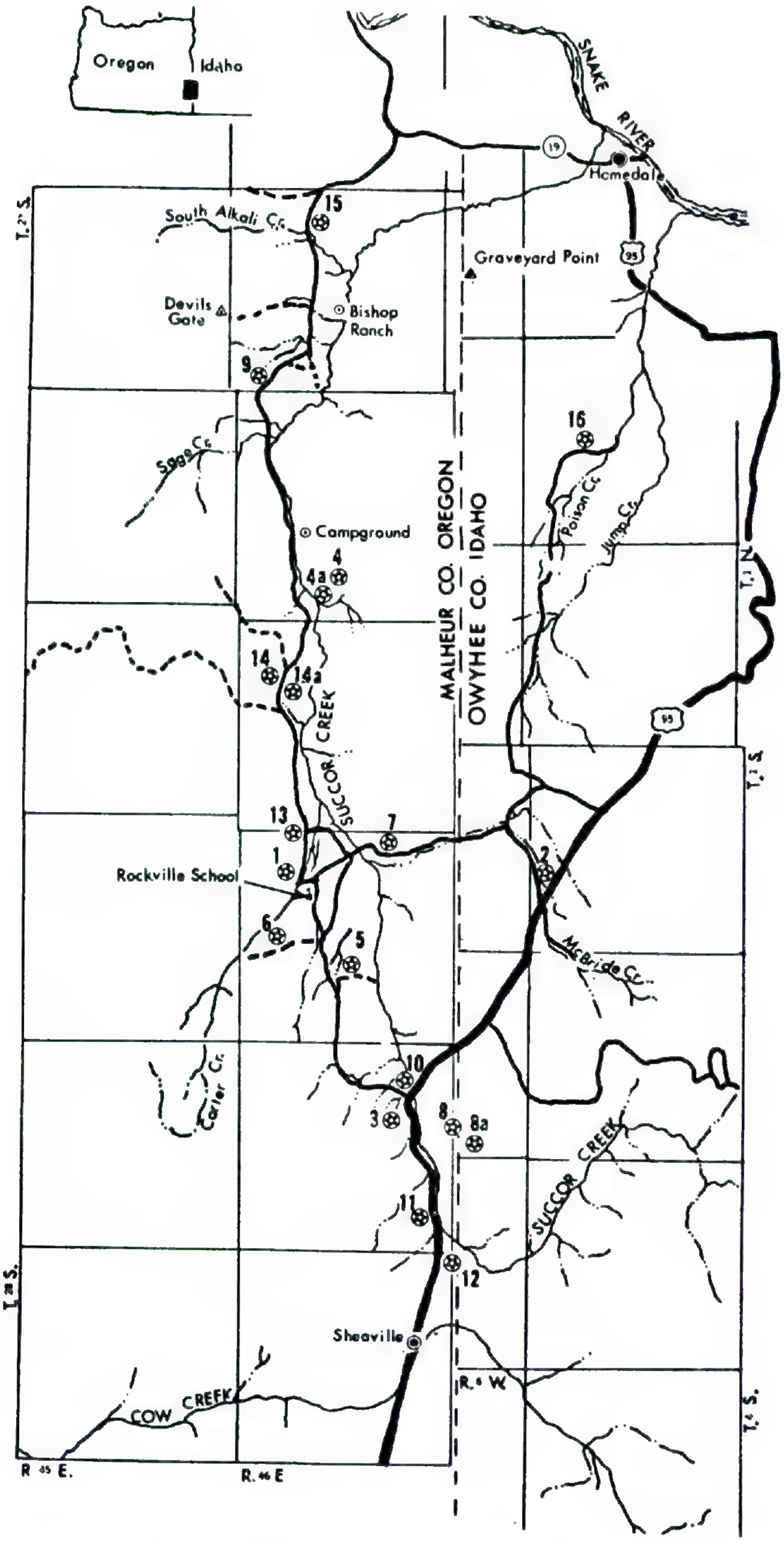


FIGURE 1. Index map of the Succor Creek area (Taggart & Cross, 1980*) showing the distribution of fossil plant localities and measured stratigraphic sections. Localities noted in this paper include the Whiskey Creek section (3), the Rockville section (1), the Shortcut section (2), the Rocky Ford (4a) and Type section (4), the Pine locality (7), and the Devils Gate section (9). * Reprinted with permission from Biostratigraphy of Fossil Plants, David L. Dilcher & Thomas N. Taylor, editors. Copyright 1980 by Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pa.

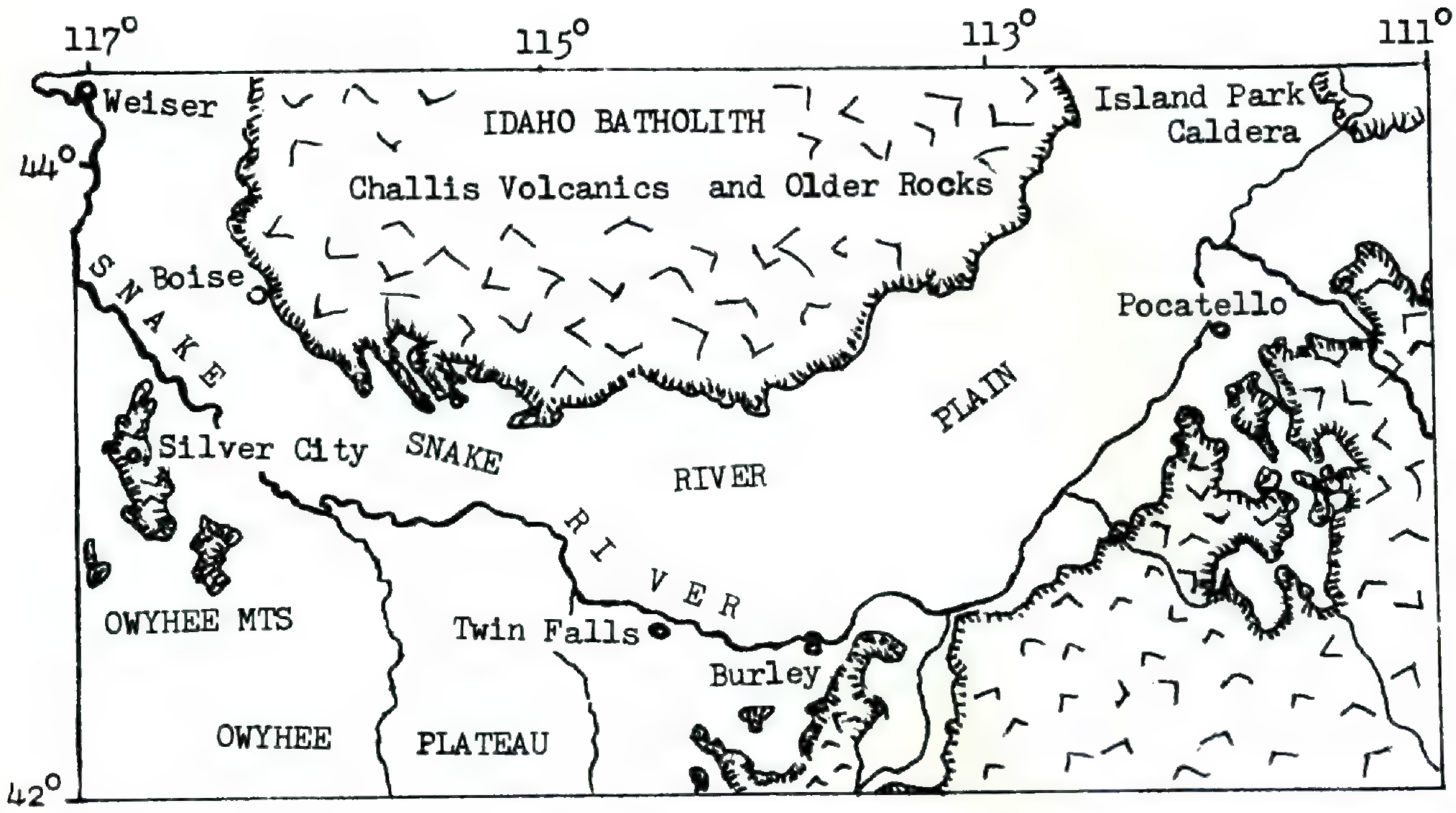


FIGURE 2. General physiographic map of southern Idaho and the Snake River Plain. The Succor Creek area lies along the Idaho-Oregon boundary between Silver City, in the Owyhee Mountains at the south, northward to about one-half the distance to the point where the Snake River intersects the Idaho-Oregon border. L-pattern area of pre-Miocene rock; hachures indicate the Owyhee Mountains and uplands bordering the Snake River Plain. (From Armstrong, Leeman & Malde, 1975, Amer. Jour. Sci. 275: 226, fig. 1.)

basalt sample taken from near our locality 3 (Fig. 1) was dated by Evernden and James (1964, p. 971, KA 1285) at 16.7×10^6 years, but neither the precise locality of the sample could later be verified by G. T. James, the collector, nor can the relationship of the basalt to the Succor Creek plant-bearing beds north of U.S. Highway 95 (near the Succor Creek bridge) be determined, because of extensive faulting in the area. This early Barstovian age agrees well with the age-determination based on mammal fossils by Scharf (1935) and Shotwell (*in* Kittleman et al., 1965, p. 7; see also Shotwell, 1968), from near the Type locality (loc. 4, possibly Unit 14, Fig. 10). Chaney and Axelrod (1959, p. 113) assigned a middle to late Miocene age to these plant-bearing beds on the basis of collections, probably taken near our locality 3 (Fig. 1). Kittleman obtained a 15.4 ± 0.9 m.y. age on sanidine and an 18.5 ± 1.7 m.y. age on glass shards from his Unit K-20 (our Unit 31) of the Type section (loc. 4, Fig. 10). Watkins and Baksi (1974) determined Normal polarity of the paleomagnetism in Owyhee Basalt, which overlies the Sucker Creek Formation in some parts of this area, with supporting age dates of 13.1–13.9 m.y.

SUCCOR CREEK FLORA

Knowlton (1898) described the first plants that were collected in this area by W. Lindgren, apparently below the base of our locality 3 and near our locality 6 (Fig. 1). Subsequently the flora was studied by Berry (1932), Brooks (1935), Arnold (1936a, 1936b, 1937), Smith (1938, 1939, 1940), and Chaney and Axelrod

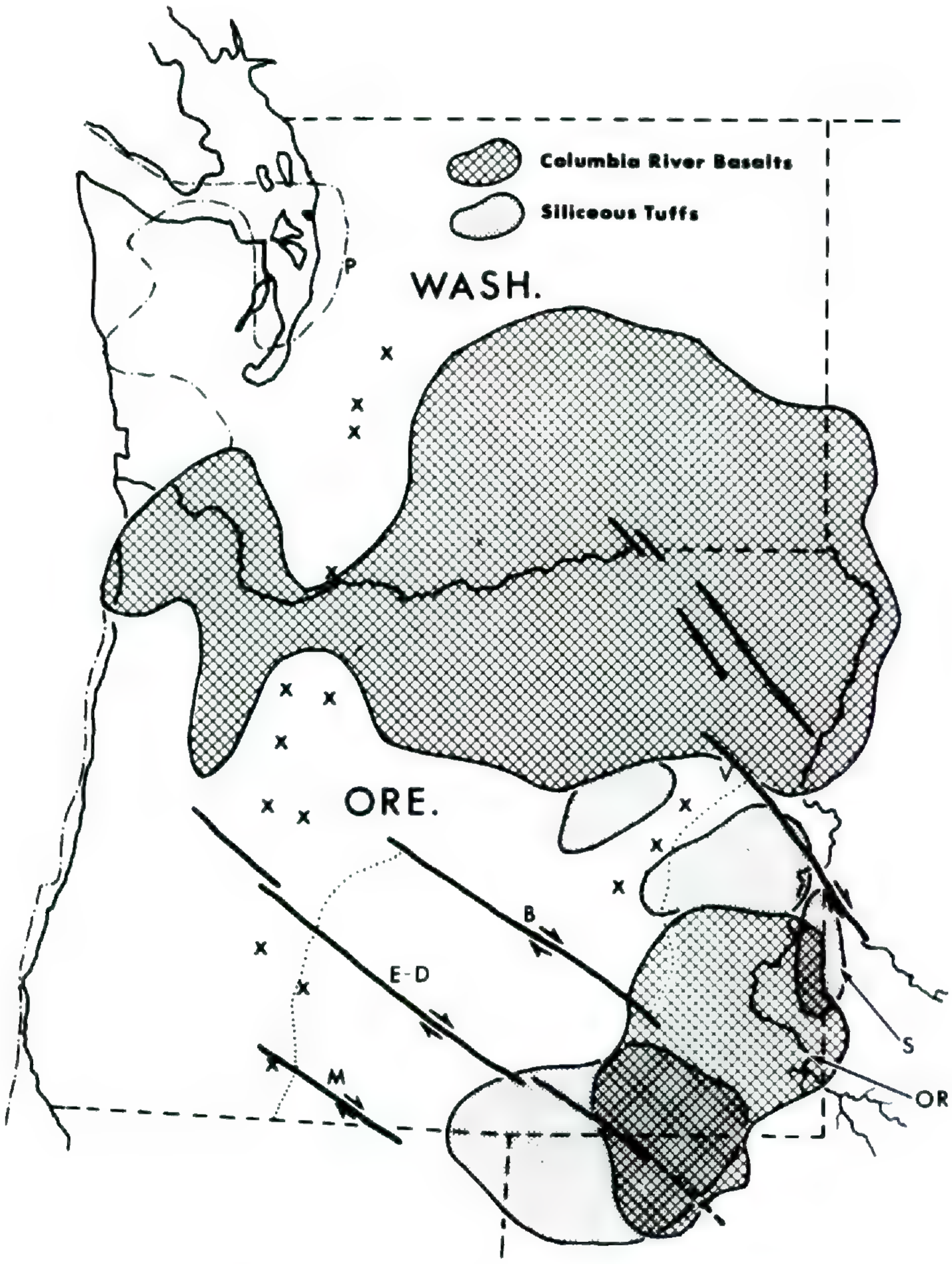


FIGURE 3. Generalized map of distribution of volcanic centers and siliceous pyroclastic tuffs, which include area of the Sucker Creek Formation (S), and the Columbia River Basalts (after McBirney, 1978, Ann. Rev. Earth Planetary Sci. 6: 439, fig. 1). Four right-lateral strike-slip fault zones extend W–NW across Oregon (M = McLoughlin zone; E–D = Eugene–Denio Zone; B = Brothers Fault zone; V = Vale zone). The western and northern margin of the Basin and Range Province is delimited here by the dotted line from south of the McLoughlin zone line north and northeast to the Brothers fault zone; thence southeast along the Brothers Fault to Steens Mountain Fault, a major normal fault trending N–NE; thence northeastward to the Vale zone (from ERTS mosaic of Oregon as shown in Lawrence, 1976, Bull. Geol. Soc. Amer. 87: 847, figs. 1–2). X = andesitic volcanic cones; ·—·—·— = Pacific Ocean boundary in Mid- to Late-Miocene; OR = Owyhee River; S = Succor Creek area. Arrows indicate the net direction of movement along faults and fault zones. The Snake River is, in part, occluded here by the line marking the Vale fault zone. The line of andesitic cones northward through Oregon and Washington marks the volcanoes of the present High Cascades.

(1959). Graham's extensive studies (1963, 1965) reported 69 species, representing 60 genera distributed among 47 families. He also conducted the first analysis of the spores and pollen in these strata. Taggart (1973) added seven new taxa to the flora.

The Succor Creek Flora is a composite of many florules based upon fossil plant specimens collected from at least 25 published localities. Historically, this

has been considered to be one flora that accumulated intermittently for a period of one to two million years over a subdued, eroded, volcanic landscape, probably a plateau. Plant remains have been preserved in intermittently deposited, largely fluvially recycled, pyroclastics, i.e., ash, ash-flow tuffs, and weathering products of basalts and rhyolites, and in some direct ash-falls. Graham (1965) in his review of the fossils collected at 16 sites, stated (p. 16) ". . . There is no evidence of disproportionate representations suggesting significant variation in the age of the localities . . . it is likely that several basins were variously connected at different times . . . ," and, ". . . It must be assumed . . . that these basins were of approximately the same age, geologically, and that the Sucker Creek constitutes a single paleofloristic unit."

One exception to this concept of a "single flora" made up of many florules was introduced by Wolfe (1969, p. 88–89) where he states, ". . . The Succor Creek (late Miocene) and Rockville (middle Miocene) assemblages are here considered as distinct . . . ." Wolfe uses the age-date of 16.7 m.y., reported by Evernden and James (1964), to verify the age of the "Rockville" as middle Miocene, but has no age-date for the late Miocene, a situation that still exists. The latter age assignment was made (Wolfe, 1969, p. 89) on the basis that he interpreted the late Miocene assemblages to ". . . represent a cooler time interval than do the middle Miocene assemblages . . . ," and thus inferred that some of the Succor Creek florules were accumulated at a later time (late Miocene?) in a cooler climate, than the "Rockville." The identity of which of the florules he considered as "Rockville" is obscure. Though "Rockville" has been occasionally used by Axelrod, and perhaps others, it has usually been a synonym for "Succor Creek." We disagree that the one part of this flora as presently known, which has been age-dated with uncertainty at 16.7 m.y.b.p., is greatly different in age than any of the other florules that comprise the total Succor Creek Flora. In fact, the rocks that have been dated by Evernden and James did not come from the Rockville area (which lies somewhere between localities 1 and 5 as depicted on Fig. 1), but 10 to 15 km south-southeast of the abandoned Rockville post office site or Rockville school, near the junction of U.S. Highway 95 and Succor Creek (near locality 3 or 10, Fig. 1). We consider the Succor Creek Flora to have been accumulated intermittently over a period of one to two million years, in episodically deposited sediments. Because we have repeatedly identified representative cool and warm florules at different levels in the same sections, there is no basis to differentiate the several florules into significantly different age levels on the premise that the cooler floras represent late Miocene age.

MATERIALS STUDIED

It is inferred, from limited geophysical data, that the subsurface on which the Sucker Creek Formation pyroclastics were deposited was an extensive erosion surface of undulating, low-relief topography, developed on volcanic rocks of probable early Miocene age that are possibly time-equivalent to the John Day beds of central Oregon. The upper surface of the Sucker Creek deposits is also extensively eroded and is overlain unconformably by the various rhyolite and basalt flows or clastics of the Idavada Volcanics. The unconformities at the base and the top of the Sucker Creek Formation each represent several million years

of exposure and erosion prior to and post-dating the deposition of the Sucker Creek Formation. The best estimates for the total time period for the deposition of the Sucker Creek Formation are between one and two million years, with deposition initiated about 15 or 16 million years ago.

It is evident that various parts of the Succor Creek area were accumulating plant-bearing ash beds intermittently during this one to two million year period. At no point in the area is a continuous stratigraphic sequence exposed that fully represents this time interval. Volcanic activity is episodic in nature and it is probable that most of the time for the Sucker Creek interval is represented by erosional unconformities and diastems where little or no sedimentation of volcaniclastics was occurring in the area. Each of the individual stratigraphic sections exposed within the area documents a specific time interval within the larger Sucker Creek interval but it need not be equivalent in time to other sections within the area. Precise correlation between sections demands comparability in the sequence of identifiable ash beds, preferably coupled with biotic data to substantiate that the sections represent the same or partially overlapping time intervals. These conditions are only rarely met. Given the complexity of volcanic deposition on a topographically variable landscape, one is typically limited to studying the time interval represented by individual sections, ranking them temporally in the longer Sucker Creek interval where data permit. Correlation is even more difficult in the case of exposures of plant-bearing ash in road cuts, gullies, and other sites with limited exposure due to the absence of associated rocks to assist in correlation. Despite such difficulties, it has been possible to trace specific ash beds in outcrop, correlating isolated exposures with measured sections in some cases.

Our postulation that the record of these mid-Miocene volcaniclastic sediments exhibit short-time increments of plant-bearing sediment accumulation and much longer time intervals (gaps) of non-accumulation, is in line with some of the principles summarized by Sadler (1981) and Van Andel (1981). We consider that the Sucker Creek Formation is comprised of a number of discrete episodes of sediment accumulation. This conclusion is based on the nature of the successive vegetation arrays which are represented through the formation by plant fossils of both macro- and microscopic size. The complexities of correlation, coupled with the time significance of diastems and unconformities in the sedimentary record, makes it unrealistic to hope that continuous documentation of the entire Sucker Creek time interval can be achieved. Nevertheless, sufficiently detailed studies of complete sections can be expected to provide a sufficient number of "time samples" to adequately assess the scope of variation in the floristics and vegetation dynamics of the plant communities of Sucker Creek time. Collections for palynologic studies were made from relatively closely-spaced samples from continuous sequences of strata. The sections were measured and described concurrent with sampling. Sedimentary characteristics such as bedding, grain size, texture, and some mineral characteristics were noted. Weathering characteristics, color and lateral continuity and variablity were described. Weathered surface materials and representative slabs and chips of rock from each level and each lithology were examined for larger plant and animal fossils at each sampling site.

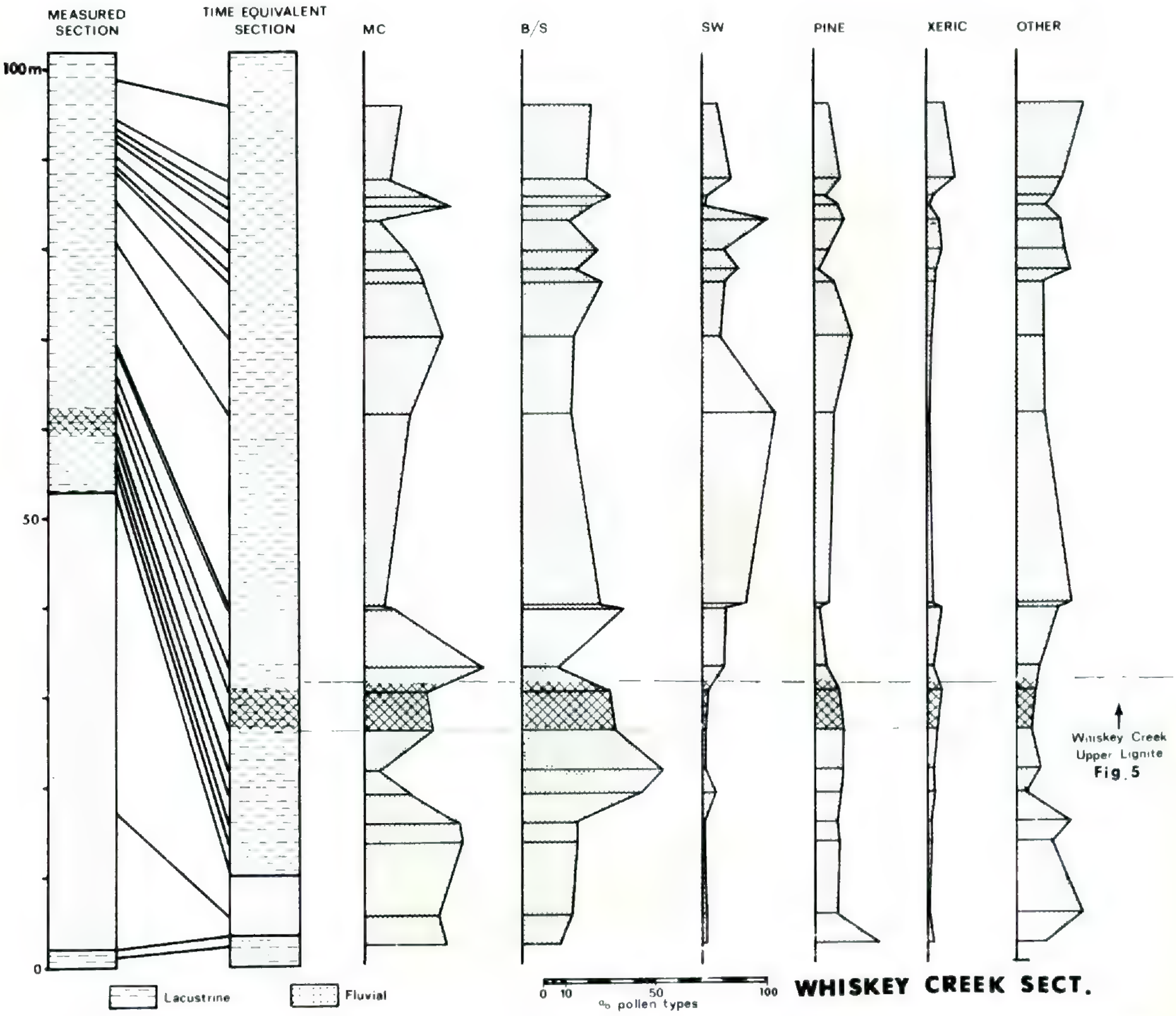


FIGURE 4. Generalized stratigraphy and relative frequency pollen data from the Whiskey Creek section. Classification of fluvial and lacustrine sediments and the rationale for the "Time Equivalent" column are discussed in the text. The following heading keys are used for the paleoassociation pollen profiles: MC, Montane Conifer Paleoassociation; B/S, Bottomland/Slope Paleoassociation; SW, Swamp Paleoassociation; PINE, Pine Paleoassociation; XERIC, Xeric Paleoassociation; and OTHER, Other Paleoassociation. The taxa constituting each paleoassociation are discussed in general terms in the text with a more detailed treatment in Taggart and Cross (1980).

The primary goal of field sampling was to assure that data were limited by the productivity of pollen and spores recovered from the samples rather than by limitations in sampling density. Repeated collections (subsampling or resampling) in subsequent field seasons were commonly made to improve the percentage of productive samples.

PERSPECTIVE

Even with the obvious limitations of the fossil record, all paleobotanists studying Neogene floras from the Pacific Northwest have been struck by the floristic diversity of the Miocene woody vegetation compared with the sagebrush-forb-steppe now occupying the region. The range of Neogene communities probably

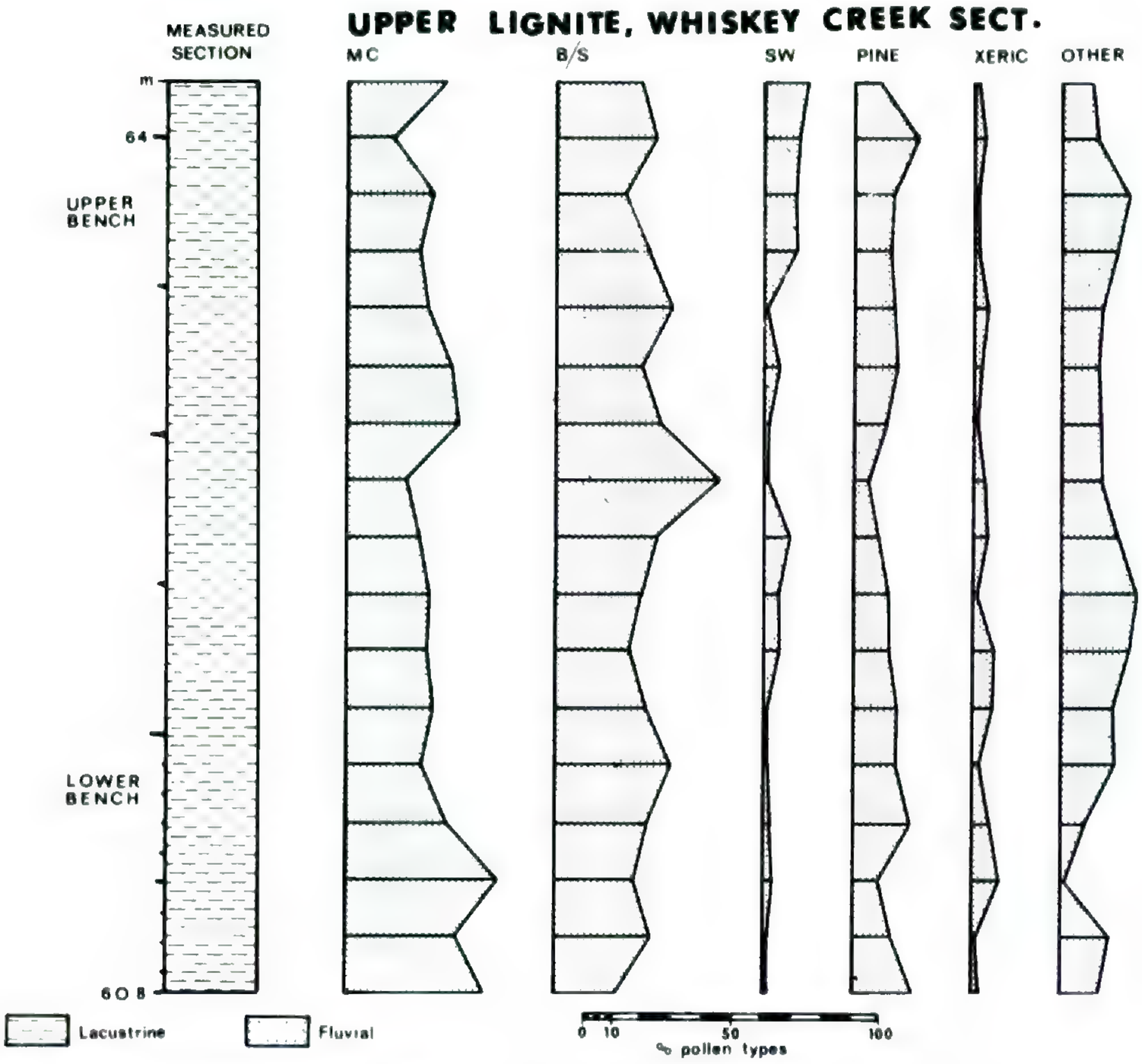


FIGURE 5. Relative frequency pollen data for the Upper Lignite sequence of the Whiskey Creek section. The paleoassociation categories follow the key in Figure 4. The "Lower Bench" and "Upper Bench" designations indicate the general position of the two channel samples representing the Upper Lignite Series in the main Whiskey Creek section profile (Fig. 4).

encompassed a floristic and physiognomic diversity comparable with the extant mesic forests of eastern Asia (Wolfe, 1979), with all of the local variability imposed by historical and site factors.

Paleobotanists have typically been sensitive to the dynamics of hydrologic succession, as these processes are intimately involved with the basins in which fossils accumulate. The work of modern ecologists on disruptive factors such as fire should sensitize us to the certainty of encountering such factors in our fossil assemblages. Similarly, our current understanding of the short-term (10^3–10^4 yr) variability in world climate would lead us to expect that similar variability might have been a factor in the past. Not as obvious, from a uniformitarian perspective, is the nature of regional disruption and widespread destruction of forest vegetation as an inevitable effect of regional volcanic activity on a scale that we have understandable difficulty in comprehending. If the floristic and physiognomic diversity of the ancient forests of this region can so obviously exceed that of the present, so too can the scope of the vegetation dynamics. We have certainly passed well through the survey phase in our study of the Neogene floras of the region and are now attempting, with various approaches, to arrive at an adequate synthesis of the vegetation history of the region. A realistic appreciation of the scope of paleoecological diversity will not confound such an effort; rather it may materially assist in arriving at a consensus derived from many lines of evidence

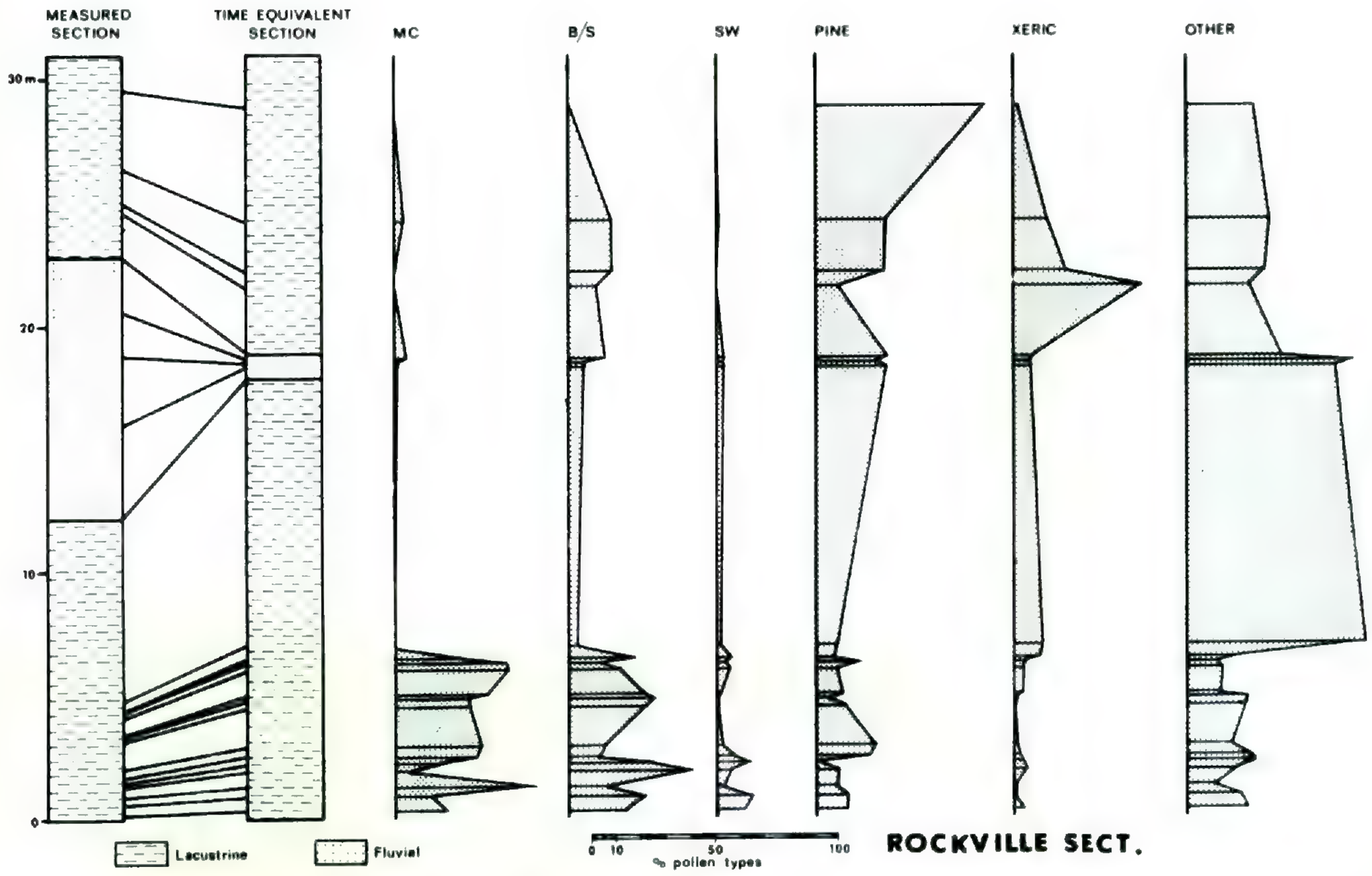


FIGURE 6. Generalized stratigraphy and relative frequency pollen data for the Rockville section. The stratigraphic display and paleoassociation key follows that of Figure 4.

that will permit us to understand rather than simply record the events that have shaped the biotic history of the region.

RESULTS

STRATIGRAPHIC PALYNOLOGY

Pollen diagrams from the Whiskey Creek section (Valley section of Taggart & Cross, 1980), the Upper Lignite of the Whiskey Creek section, and the Rockville, Shortcut, and Type sections are contained in Figures 4–8. These figures incorporate several common elements in a new type of data display that is briefly discussed below.

Measured Stratigraphic Column.—Each figure contains a generalized stratigraphic column summarizing the depositional environment during the period represented by the measured section. Two general sedimentary environments are recognized. Coarse to fine volcanic sandstones and siltstones in this region are considered to represent fluvial depositional environments, and shales, mudstones, and lignites are collectively grouped as representative of lacustrine deposition.

"Time Equivalent" Column.—It is well known that sediments accumulate at different rates in different sedimentary environments, a topic to be further discussed under "Shifts In Community Distribution: Time Factors." Typically thicker deposits of coarser-grained fluvial sediments will accumulate more rapidly than the finer-grained lacustrine sediments. In order to approach a more realistic portrayal of the relative time represented by interbedded fluvial and lacustrine units

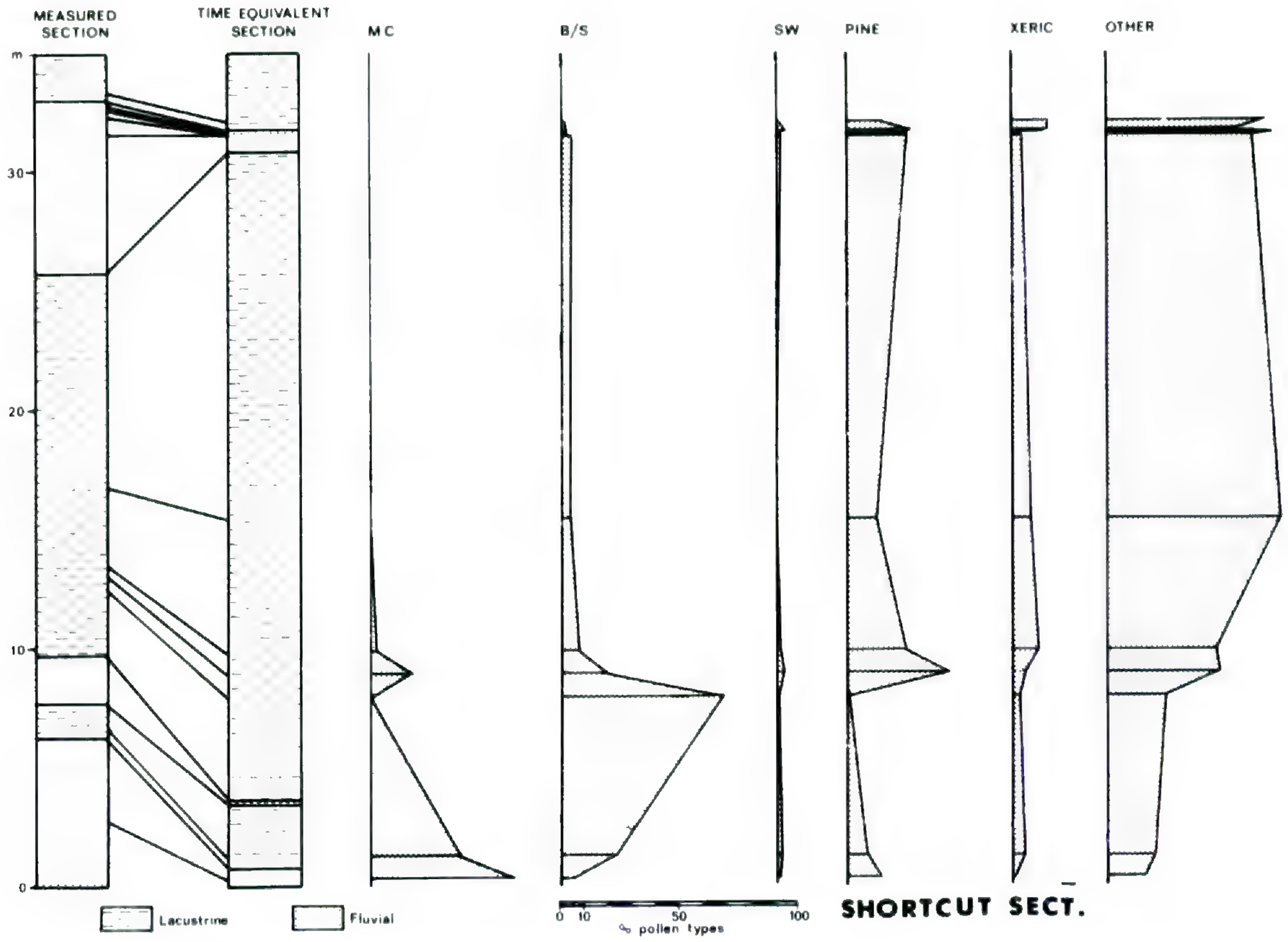


FIGURE 7. Generalized stratigraphy and relative frequency pollen data for the Shortcut section. The stratigraphic display and paleoassociation key follows that of Figure 4.

in a stratigraphic section, the lacustrine units were arbitrarily expanded vertically by a factor of 15 (see discussion under Time Factors: Relative Time Equivalents, etc.), followed by the application of a constant correction factor to all units to re-scale the display (2nd columnar section) to the equivalent of the measured section diagram in each of Figures 4–8. This "time equivalent" column is included to provide a rough approximation of the relative time period represented by the various rock units in each section.

Sample Productivity.—All samples were processed to separate the palynomorphs from the sediments but only those samples yielding sufficient pollen and spores for quantitative treatment are included on the diagrams. Generally 15% to 30% of the samples obtained from each section were productive, with recovery from lacustrine sediments significantly better than from the volcaniclastic dominated fluvial deposits. All samples from the Upper Lignite sequence in the Whiskey Creek section (3 m of organic mudstones, siltstones, and impure lignite) were productive. The positions of all productive samples for each section are plotted on the "Measured Stratigraphic" column for each section as well as on the "Time Equivalent" column.

PALEOASSOCIATIONS

All taxa found during sample tabulations were ultimately recorded in terms of their relative percent contribution to the total pollen and spore count, excluding

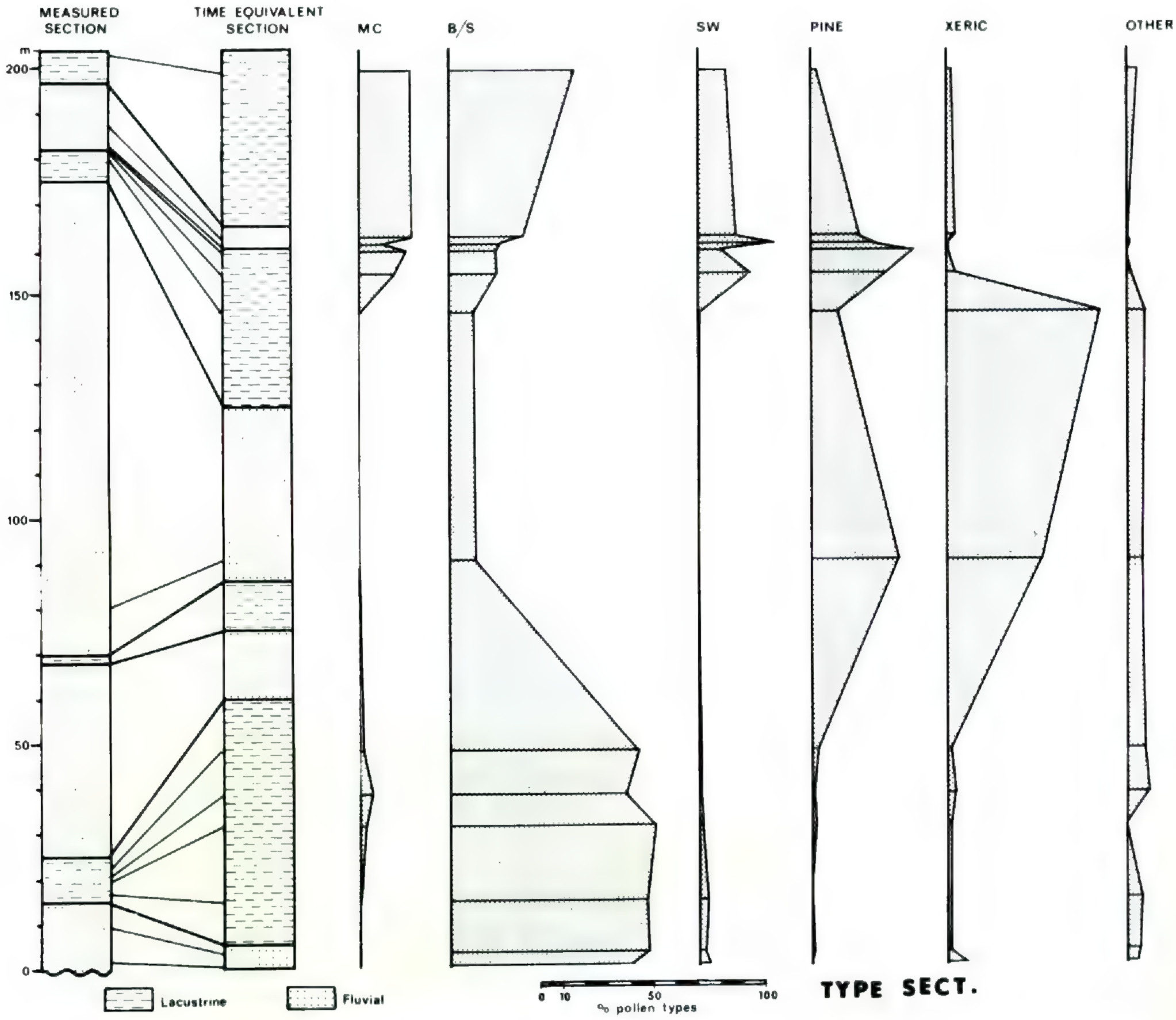


FIGURE 8. Generalized stratigraphy and relative frequency pollen data for the Type section. The stratigraphic display and paleoassociation key follows that of Figure 4.

algal and fungal entities. Over 75 discrete pollen types including 55 genera in 36 families have been encountered in the study sections. The relative frequency pollen diagrams are thus quite complex. The total flora of leaves, fruits, seeds, pollen, and spores from the Sucker Creek Formation now exceeds 50 families.

In order to simplify data display, the various pollen types have been grouped into six generalized "paleoassociations" on the basis of general association of similar source plants in extant communities (Taggart & Cross, 1974, 1980). The Montane Conifer Paleoassociation consists of the pollen of *Picea*, *Abies*, and *Tsuga*, with dominance reflected in this ordering in virtually all cases. All *Pinus* pollen types are grouped into the artificial Pine Paleoassociation based on the wide ecological amplitude of pine species coupled with the difficulty in obtaining precise taxonomic resolution in this complex. The Swamp Paleoassociation is dominated by pollen of the Taxodiaceae, with the pollen of *Typha*, the Nymphaeaceae, and *Potamogeton* included as very minor marsh and aquatic elements. Most of the taxodiaceous pollen is probably attributable to *Glyptostrobus*, which is well-represented by macrofossil material throughout the Succor Creek region.

Taxodium leaf material has, however, been collected at two sites, so a role for *Taxodium* as a possible source plant for taxodiaceous pollen must be considered. The Xeric Paleoassociation includes the pollen of the Chenopodiaceae/Amaranthaceae, Compositae, Gramineae, Leguminosae, Malvaceae, and Onagraceae, plants now associated with somewhat xeric or disturbed habitats. The Bottomland/Slope Paleoassociation is the most diverse, including the pollen of approximately 20 genera of predominantly broad-leaved trees and some shrubs. The important plants of this paleoassociation are *Ulmus*, *Quercus*, *Alnus*, *Carya*, *Pterocarya*, *Betula*, *Acer*, *Fagus*, and *Juglans*. The sixth category, "Other," is completely artificial and includes the pollen of undifferentiated bisaccate gymnosperms, some unknown but presumably angiospermous pollen types, and undeterminable pollen grains.

The 100 m Whiskey Creek section (Fig. 4) is characterized by oscillations between the Bottomland/Slope and Montane Conifer Paleoassociations. A peak in Swamp pollen near the middle of the section corresponds to the "Valley Plant Beds," an exposure yielding a diverse assemblage of broad-leaved taxa and numerous specimens of *Glyptostrobus*.

The Upper Lignite Series is one of two 3 m lignite and lignitic shale units near the middle of the Whiskey Creek section. The upper unit (Fig. 5) was sampled at 20 cm intervals and indicates a pattern of mild oscillations between the Montane Conifer and Bottomland/Slope elements. There is a gradual trend toward increasing Swamp pollen toward the top of this unit, consistent with the initiation of the Swamp peak in the main Whiskey Creek section.

The Rockville (Fig. 6) and Shortcut (Fig. 7) sections are correlatable throughout most of their thickness and show similar pollen profiles. The basal part of each section is dominated by the pollen of the Montane Conifer and Bottomland/Slope elements but each section shows an abrupt transition marked by the disappearance of the Montane Conifer element and a drop in the number and diversity of Bottomland/Slope pollen. Above this transition the Rockville section shows a pattern of sequential dominance by Other (unknown angiospermous pollen types), Xeric, and Pine Paleoassociations. The Pine maximum at Rockville correlates with the nearby "Pine Locality" where abundant leaf fossils of two- and three-needle pines have been collected.

The Type section diagram (Fig. 8) shows an initial period of Bottomland/Slope pollen dominance, followed by a transition to Xeric and Pine dominance. The upper Type section records an increase in the number and diversity of Bottomland/Slope pollen types, co-dominant with Montane Conifer pollen. The Bottomland/Slope Paleoassociation in the upper Type section is oak-dominated in contrast to elm-dominated spectra from the lower Type section and the other study sections. A leaf bed from the upper Type section is also somewhat atypical in that it is dominated by *Ulmus* and *Salix* and contains leaves of *Carya* and *Populus* cf. *pliotremuloides*, the only Succor Creek leaf records for these latter two taxa.

We have also studied the Rocky Ford section, an 11.2 m lacustrine unit outcropping across Succor Creek about 375 m to the west of the base of the Type section exposure. If dips are consistent across the Succor Creek valley, field measurements indicate that the top of the Rocky Ford sequence correlates to within 2 m of the base of the Type section. Two productive samples were re-

covered from the Rocky Ford sequence. Both are similar in composition, averaging 39% Montane Conifer, 47% Bottomland/Slope, 1.5% Swamp, 9% Pine, 1% Xeric, and 2.5% Other pollen. Palynologically, the Rocky Ford samples are indistinguishable from those of the Whiskey Creek and lower Rockville and Shortcut sections but are quite different from the Bottomland/Slope dominated spectra of the basal Type section. Thus, although structural indications point to only a slightly earlier age for the Rocky Ford sediments, relative to the basal Type section, the possiblity of faulting, a diastem or an unconformity must be considered.

SUMMARY OF DATA DISPLAYED IN FIGURES 4–8

Three main pollen/spore assemblages have been differentiated in the sections studied and have been plotted on a time equivalent base.

1. *Co-dominance of Montane Conifer and Bottomland/Slope Paleoassociations*.—There is often considerable variation in the relative importance of these two elements where they co-occur. Swamp pollen may increase to significant levels at times. Pine and Xeric elements are typically minor. This assemblage is characteristic of the entire Whiskey Creek section, the lower Shortcut and Rockville sections, the Rocky Ford section, and the upper Type section.

2. *Dominance by the Bottomland/Slope Paleoassociation*.—Bottomland/Slope element ranging from 75% to 90% for an extended period of time; Montane Conifer pollen virtually absent, and other elements are of minor importance. This is an assemblage that has been found only in the lower Type section and at several intervals in the lower Devils Gate section.

3. *Xeric/Pine Assemblage*.—Pollen record dominated by Xeric and Pine Paleoassociations, including the "Other" category when the latter is dominated by pollen of plants of unknown but presumably herbaceous affinities. Montane Conifer pollen typically lacking, with Swamp pollen at low levels. Bottomland/Slope representation is typically low in both numbers and diversity.

DISCUSSION

A CONCEPTUAL FRAMEWORK FOR ECOLOGICAL RECONSTRUCTION

The Clements (1916) concept of "climax" vegetation is simple in its most basic form, i.e., the vegetation type of a region that exists in equilibrium with the prevailing climatic regime. However, the concept becomes complex when applied to real plant distribution. Most ecologists now recognize that the climatically controlled vegetation of any region is in reality a complex mosaic with the distribution of community types controlled by a wide variety of factors. These include elevation, slope exposure and other edaphic factors, microclimatic amelioration, the biotic potential of the region, past community distributions, and the degree and timing of events acting to disturb or disrupt community structure. Documentation of the nature of the climax mosaic is complicated throughout much of the northern hemisphere because many vegetation types may not have reached equilibrium since the most recent Pleistocene glacial maximum. Recent data also suggest that, on the scale of the centuries, climate is not stable. Fur-

thermore, the size of natural communities, coupled with disturbances such as fire and human intervention, may preclude the "steady state" inherent in the climax concept (Bormann & Likens, 1979). Shugart and West (1981) note that "forest ecosystems are dynamic entities that may not be static in either time or space. Many of our concepts are based on the hope that if a forest is left alone it will gradually return to its natural state." They also note that, ". . . 'succession,' 'wilderness,' 'virgin forests,' and 'climax forests,' are all concepts that appeal to the basic notion that forest systems should approach some equilibrium state with time . . . ." They state that, ". . . research indicates that forests in highly disturbed landscape may remain in perpetual state of effective non-equilibrium and that if the scale of disturbance is large, then the amount of land required to absorb the effects of the disturbance is also large" (p. 647).

Paleobotanical analysis of Tertiary floras is directed toward understanding the floristics of fossil assemblages and the type and distribution of the ancient plant communities and to utilize the data to reconstruct the climate of a region. This has been the case with the Neogene floras of the Pacific Northwest where two principal approaches to paleoclimatic reconstruction have been utilized. In the paleoecological approach, typified by such works as that of Axelrod and Bailey (1969), an attempt is made to reconstruct the nature of thermal conditions that controlled floras by analysis of the ecological affinities of the fossil plants. Others (e.g., Wolfe, 1978) utilize leaf physiognomy as a climatic indicator in an attempt to avoid limitations in our understanding of the floristics of an assemblage and the unknown factors of ecological constancy of taxa with the passage of time.

These two approaches have yet to converge on a consensus regarding the pattern of Neogene paleoclimatic dynamics. It is not our intention here to argue for one approach or the other but there is an *a priori* assumption inherent in both approaches, that the floras under study represent a mosaic of vegetation types in a steady state or "climax" equilibrium with climate. If this assumption is not the case, then the flora under study cannot provide a reliable indication of the climate under which the flora was developed. It is also assumed that changes in climate, which would shift the nature of this equilibrium, are not operating within the time period represented by a single flora but can be resolved by comparisons between floras of different ages. Such conditions may pertain for some fossil plant assemblages, but it is our contention that many Neogene floras of the Pacific Northwest probably do not meet the conditions required to make the assumption that a relatively steady state equilibrium between vegetation and climate existed in such floras.

The preservation of the fine suite of floras in the region is due to an interval of intense volcanic activity throughout the area that has no parallel in historical human experience. It is unrealistic to assume that such vast outpourings of volcanic debris would have uniformly preserved samples of climax vegetation. If any particular area on the earth's surface today were subjected to such massive disturbance, a modern ecologist would expect the vegetation of the region to reflect the magnitude and episodic nature of the disturbances with a variety of communities reflecting successive seres leading to varying degrees of climax equilibrium with the prevailing climatic regime. In such an area, relative stability in vegetation distribution might well be the exception rather than the rule. Our

studies indicate that this appears to have been the case in southeastern Oregon and southwestern Idaho during Sucker Creek time. Our data (Fig. 9) do provide indications as to the scope of the climax vegetation mosaic for the region but also record a number of disturbance factors that have served to disrupt or modify the distribution of plant communities including:

1. Hydrologic succession, involving the formation, eutrophication, and infilling of ponds and lakes, initially formed largely by damming due to ash falls, lava flows, and possibly by earthquake induced landslides.
2. Post-disturbance succession of at least two types:
   A. Disruption of vegetation by ash falls, gas venting, and mudflows associated with local and regional volcanic activity.
   B. More localized forest disruption by fire.
3. Cliseral shifts in vegetation distribution induced by thermal oscillations of small magnitude, possibly coupled with shifts in the precipitation regime, which are sufficient to mask any long-term trends in climatic change through Sucker Creek time.

THE NATURE OF SUCCOR CREEK CLIMAX VEGETATION

The macrofossil record for the Succor Creek Flora indicates a diverse broad-leaved forest with a restricted representation of montane conifers (spruce, fir, hemlock, and pine), identified by a small number of seeds, presumably carried into the basin by streams draining higher elevations. The presence of several genera whose extant representatives are sensitive to frost, such as *Cedrela, Persea,* and *Hiraea,* led Graham (1965) to suggest that the Succor Creek assemblage represented a warm temperate forest in which frost was rare and of short duration. The very strong deciduous aspect of the Succor Creek Flora was supported by Axelrod (1968). He mapped the Succor Creek Flora as part of a "slope forest" unit and created an eastward salient on the map of the distribution of the unit (Axelrod, 1968, fig. 7B) to accommodate the Succor Creek macrofossil data.

Palynological investigations of the flora and additional macrofossil studies of many more localities at stratigraphically oriented sites indicate that classification of the Miocene regional vegetation in the Succor Creek area as primarily broad-leaved forest is inappropriate and that greater attention must be given to the role of montane conifers in reconstruction of undisturbed Succor Creek vegetation. The pollen of spruce, fir, pine, and hemlock, assumed to have variable significance in montane forests, is routinely encountered. This discussion of climax vegetation will exclude consideration of pine. Pine pollen can be dispersed over a very large geographic area and may be carried upward or downward from source areas in large amounts (King, 1967). Leopold (1964) suggested that pine pollen percentages bear little relationship to the importance of pine in standing timber and virtually all studies of modern pollen rain support the cosmopolitan distribution of pine pollen in regions where pine is present. Our own studies of a transect of five stations in the Mt. Mitchell area of North Carolina (Table 1) show pine pollen percentages ranging from 7% to 11%, irrespective of whether pine was present in the forest vegetation surrounding the collection site. Pine pollen is invariably present in Succor Creek pollen preparations but, with the exception

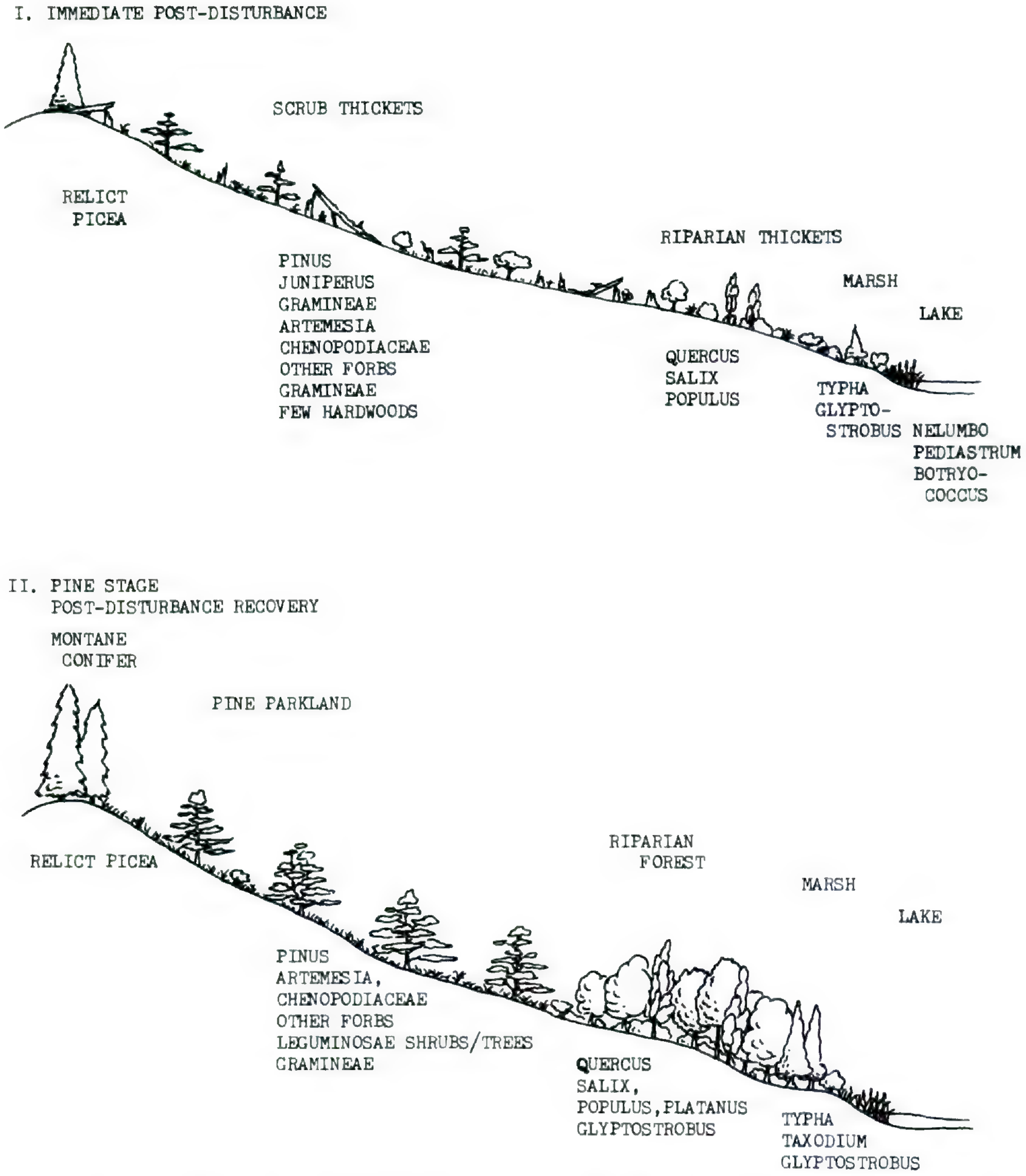
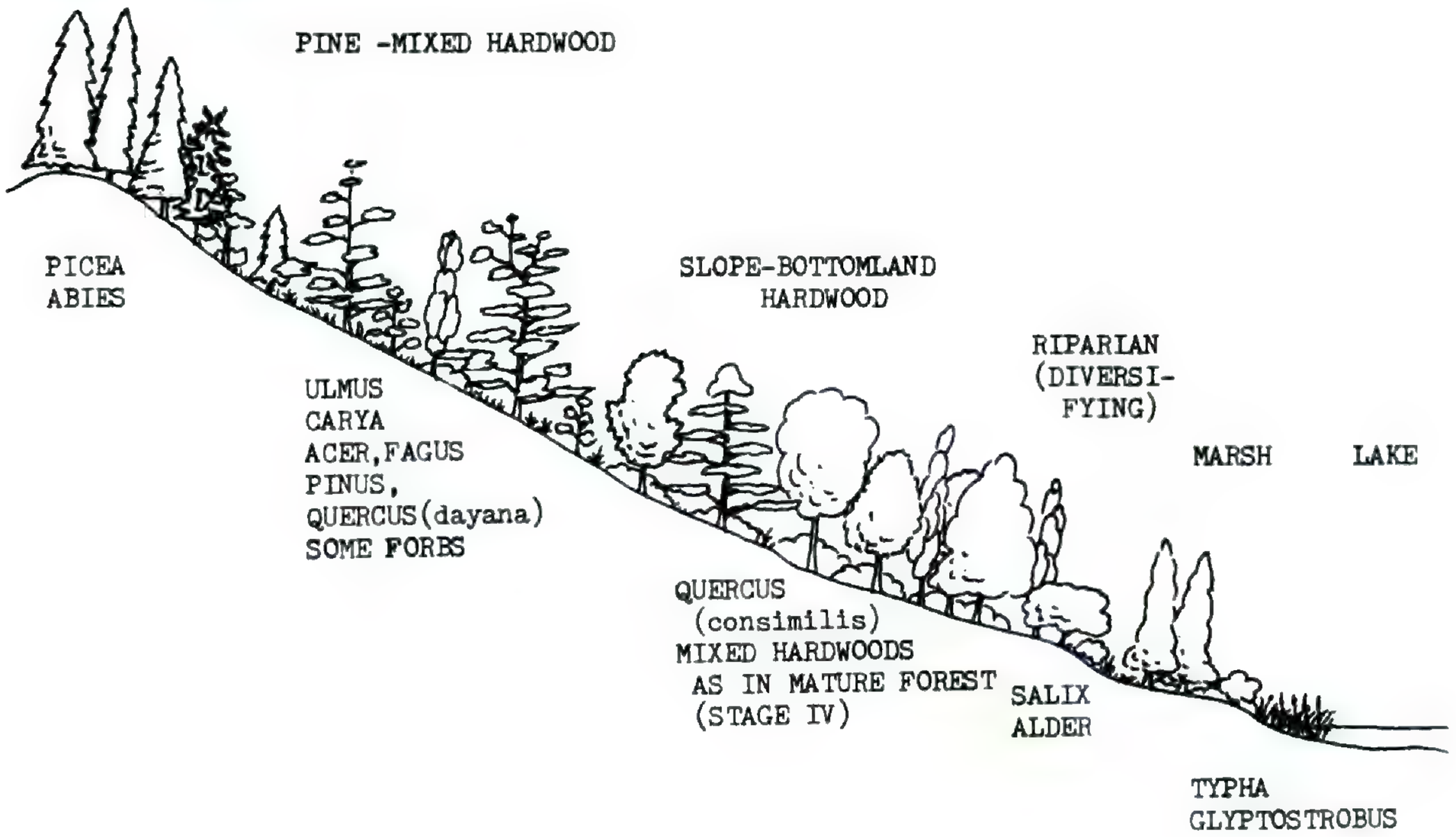
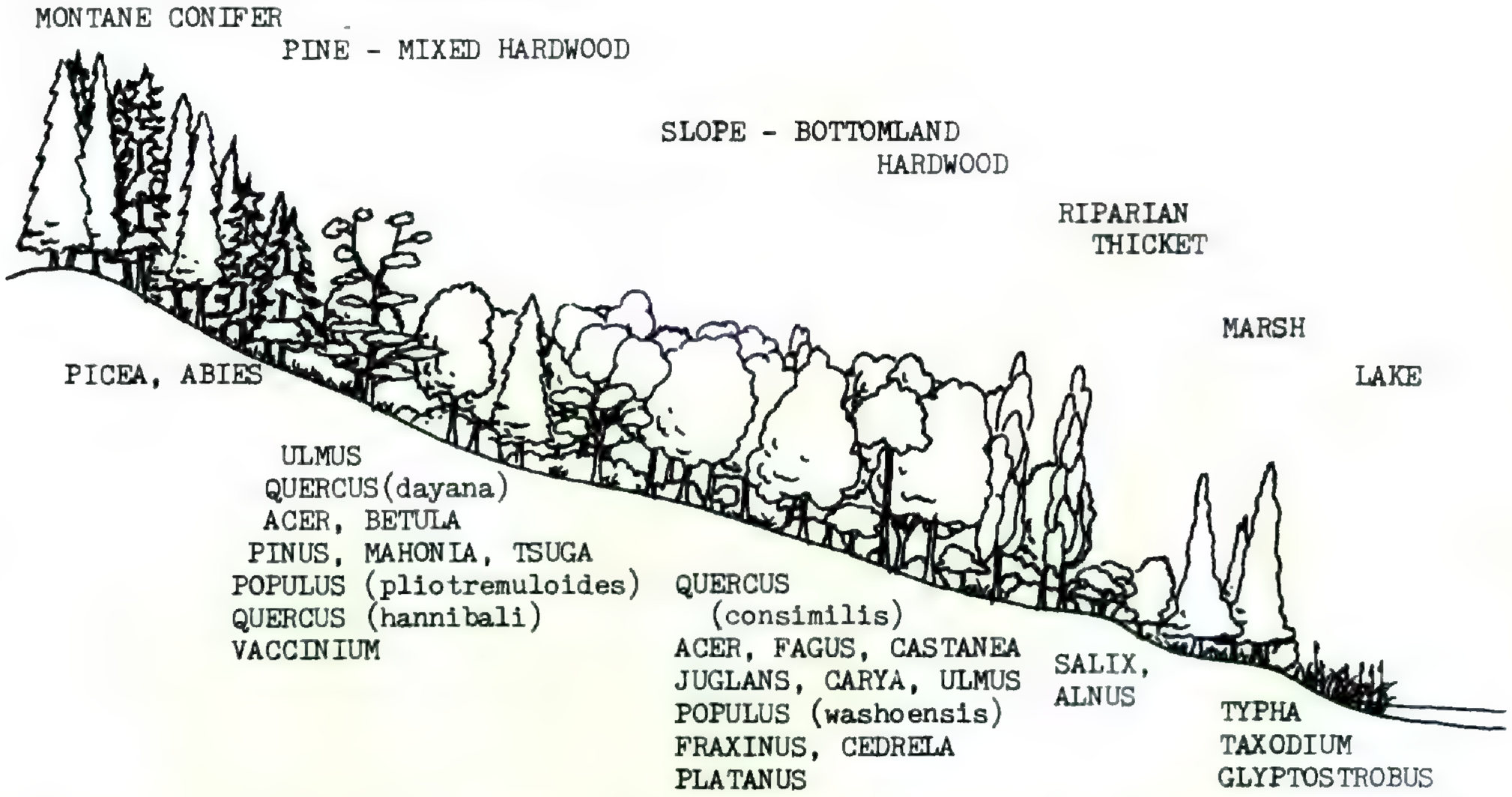


FIGURE 9. Generalized reconstructions of Succor Creek vegetation distribution at various stages following massive volcanic disturbance. I. The vegetation array shortly after disturbance with a limited riparian assemblage surrounding the depositional basin with most of the area dominated by a grass-forb complex with seedlings of trees and shrubs becoming established. II. The "Pine Stage" in the recovery sequence with a more diverse riparian forest in the lowlands and the development of a pine-parkland on surrounding slopes. III. A late post-disturbance stage with progressive development of

of its marked presence in the post-disturbance vegetation, the pine pollen component can be considered as background, derived from trees sparsely scattered through the forests at various elevations.

The pollen of spruce, fir, and hemlock, which we have previously grouped together as the Montane Conifer Paleoassociation (Taggart & Cross, 1980), is significant however. Although Graham (1965) was the first to note the presence





lowland forests, successional deciduous forests on low slopes (possibly with extensive pure stands of *Carya* and *Liquidambar*), and re-development of the montane conifer forests at higher elevations. IV. This portrays essentially "climax" or steady-state community distribution with well-developed conifer forests on the low hills, grading into broad-leaved forests on the lower slopes and into the bottomlands surrounding the basins of deposition.

of these conifers in the Succor Creek pollen record, the data did not influence his interpretation of the flora as warm temperate. We have noted (Taggart & Cross, 1980) that, where present, the pollen of the Montane Conifer Paleoassociation averages 25%, reaching peaks of 50% to 60% in some sections. To account

TABLE 1. Modern pollen rain, classified according to the Succor Creek Paleoassociations (Taggart & Cross, 1980) for five stations in the area of Mt. Mitchell, North Carolina (U.S.A.).

Elevation	Vegetation	Pollen Spectrum				
		Montane Conifer	Bottom-land/ Slope	Pine	Xeric	Other
2,013 m	Fir-spruce forest	26	53	11	10	0
1,739 m	Deciduous forest, spruce common	10	69	11	9	1
1,586 m	Deciduous forest, spruce present	4	78	14	4	0
1,452 m	Deciduous forest, hemlock present, spruce erratic, scattered pine	4*	76	7	13	0
1,037 m	Deciduous forest, scattered hemlock, scattered pine	5*	80	9	6	0

* Hemlock dominated.

for this significant montane conifer component we have interpreted the vegetation as having been developed on a topographically diverse landscape, with low-slope gradients, under a cool but highly equable climatic regime. Small thermal oscillations would have resulted in minor elevational shifts in the ecotone between the conifer and broad-leaved forests, which, when coupled with low-slope gradients, would result in pronounced changes in the distance between the ecotone and the depositional basin. These small elevational but widespread areal shifts would produce the pronounced inverse oscillations in the relative representation of the two paleoassociations in the pollen record.

Our reconstruction is greatly influenced by the levels of Montane Conifer pollen noted in our spectra. Our interpretation might be viewed as overstating the importance of pollen that some consider to have been carried into the basin from a considerable distance (e.g., Axelrod, 1965, p. 169). Such a view is often based on an appreciation of the wide dispersal range of pine pollen and the supposition that the pollen of other conifers with vesiculate pollen must behave similarly. Leopold (1964) noted that spruce pollen percentages are roughly comparable to the relative representation of the species present in area forests and that fir pollen is greatly under-represented. King (1967) noted that the proportion of spruce in the total pollen rain diminishes very quickly outside of the area of spruce occurrence in the Sandia Mountains of New Mexico and similar results were obtained by Dixon (1962) and Maher (1963) from the Sangre de Cristo Mountains of New Mexico and the San Juan Mountains of Colorado. Potter and Rowley (1960) noted the virtual absence of spruce pollen in the modern pollen rain of the San Augustin Plains of New Mexico, despite the presence of a 400 hectare stand of spruce located approximately 22 km from the border of the drainage area. They state that any significant amount of spruce pollen in a sedimentary profile would indicate the near presence of spruce.

In one of our own studies, used here to typify pollen dispersal in a more densely forested region, a collection of moss polsters was made at five stations

on Mt. Mitchell in the Blue Ridge Mountains of North Carolina. The dominant regional vegetation is of the Mixed Mesophytic Forest Association with spruce-fir montane forests developed progressively above 1,500 m. The results, with pollen taxa grouped into associations comparable to the paleoassociations used in our Succor Creek study, are shown in Table 1. At the highest station, just below the Mt. Mitchell summit (2,013 m) in a closed canopy fir forest (*Abies fraseri*) with scattered spruce (*Picea rubens*), Montane Conifer pollen reaches 26%, roughly equivalent to the *average* representation of the comparable paleoassociation in the Succor Creek record. The Montane Conifer assemblage drops to 10% at 1,739 m, despite the fact that spruce is a common forest component at this level. At 1,586 m and lower on the slopes, the Montane Conifer element drops to quite low percentages with the majority at lower elevations composed of hemlock pollen in forests where hemlock is commonly present. Even at the summit in a closed-canopy conifer forest, the conifer pollen rain is diluted by the massive influx of pollen derived from the extensive regional deciduous forest.

Given the 25% average representation of Montane Conifer pollen in the Succor Creek record, with peak spectrum values of 50–60%, long-range transport of this pollen is simply not to be expected. The megafossil record makes it clear that the vegetation surrounding the basin was a broad-leaved forest, yet Montane Conifer pollen levels are comparable to and typically exceed those noted in the conifer forest in the North Carolina collections. The relatively high conifer pollen levels in the Succor Creek Flora indicate massive pollen rain from a regional spruce-fir forest that is diluted by the deciduous forest pollen produced locally at lower elevations in the valley systems.

A flora under study from the nearby Reynolds Creek watershed of Idaho provides additional collateral data bearing on the question of the Succor Creek thermal regime. The Reynolds Creek deposits are considered equivalent in age to the Sucker Creek and yield pollen spectra comparable to those from Whiskey Creek, lower Rockville and Shortcut, Rocky Ford, and upper Type sections, including Montane Conifer Paleoassociation pollen values from 0 to 24% (mean of 7.2%). Diatoms we have recovered from our Reynolds Creek samples are currently under study by J. Platt Bradbury, of the U.S. Geological Survey, and appear to indicate the presence of a cool, shallow-water environment (Bradbury, pers. comm., 6 January 1981). We have also isolated zygospores of *Mougeotia* (Zygnemataceae) from these samples. van Geel and van der Hammen (1978) note the recovery of *Mougeotia* zygospores from the Quaternary of the Colombian Andes and its modern occurrence at sites between 2,100 and 4,500 m. Hoshaw (1968) noted that optimum growth temperature for the genus falls between 10° and 15°C. Round (1965) cited numerous occurrences of *Mougeotia* in algal communities of ponds, lakes, and rivers with most examples drawn from sites in cool to cold climates. Cool, shallow-water habitats suggested by fossil algae in the Reynolds Creek strata are consistent with our climatic reconstruction but such conditions would be quite restricted seasonally if the climatic regime were warm temperate.

Axelrod (1976) presented a large body of evidence re-interpreting the significance of montane conifers as "sub-alpine" forest indicators. Macrofossil evi-

dence of genera such as *Abies*, *Picea*, *Pseudotsuga*, *Tsuga*, and many species of *Pinus* has led to suggestions of high altitude source areas supporting sub-alpine conifer forests with isolated needles and seeds being transported relatively long distances to lowland basins of deposition. Axelrod argues persuasively that fossil remains of such conifers represent diverse conifer-hardwood forests located relatively close to the lowland depositional basins and that where sufficient relief was present, such mixed forests would become ecotonal to true sub-alpine conifer forests. Our data support his generalized reconstruction with perhaps even stronger emphasis on the role of conifers in the regional vegetation. In our flora, the lack of geological evidence for alpine topography, coupled with the very high percentage of montane conifers, would suggest that extensive conifer forests were developed at moderate elevations throughout the area, probably with a variety of ecotones between the montane conifer forest(s) and the predominantly broad-leaved forests of low slopes and lowlands (Fig. 9-IV). This is consistent with the pollen records from the Whiskey Creek, lower Shortcut and Rockville and the Rocky Ford sections, and the upper part of the Type section. A more detailed description of the diverse communities making up the lowland deciduous forest is given in an earlier publication (Taggart & Cross, 1980). The Montane Conifer element is essentially lacking in the spectra from the lower Type section, a matter of possible significance to be discussed within the topic of cliseral changes.

HYDROLOGIC SUCCESSION

The various paleoassociations that are identified from the pollen record of the Whiskey Creek, lower Rockville, and lower Shortcut sections show patterns of interaction indicative of shifts in the mosaic of vegetation types dominating the landscape during Sucker Creek time. One such event is identified by the pronounced peak in the Swamp Paleoassociation (largely pollen of the Taxodiaceae) in the Whiskey Creek section (Fig. 4) from thinly laminated shales of probable lacustrine origin. Several types of algae (*Botryococcus*, *Pediastrum*, and diatoms) are evidence for the presence here of ponds or lakes, formed by impoundment of streams by extrusives or mud or ash flows. The most likely explanation for the swamp pollen peak in this section is the occurrence of a hydrologic succession linked with the eutrophication of the pond or lake. In this case the swampy margins of the aging lake supported increasingly extensive stands of *Glyptostrobus* and possibly *Taxodium*. Ultimately the lake basin filled with sediments, including the peats, and the old lake area gradually became a bottomland habitat with the penecontemporaneous decline in the abundance of *Glyptostrobus* pollen transported to the basins of deposition. This example of hydrologic succession may also provide a rough calibration of the time interval represented by the shales of the Whiskey Creek section and, by inference, a rough guide to the sedimentation rates for other sections in the area. The process of eutrophication can require as little as a century for a small lake and up to many thousands of years for large lake systems. As there is no available geological evidence supporting the existence of very large lakes in the Succor Creek area, it is reasonable to assume that the Whiskey Creek lake(s) was of limited size and may have filled in within a thousand years or so. If this was the case, the 50 m shale and siltstone sequence in the upper part of the Whiskey Creek section was probably accu-

mulated within a very short time, geologically, i.e., a few thousand to ten thousand years. Swamp pollen peaks are noted in most sections but they are of less magnitude and shorter duration than that of Whiskey Creek. This indicates that most lakes or ponds were of small size. It is possible that some may have been prematurely drained by breaching of the containment feature (lava dam, mud flow, ash fall, etc.), which resulted in termination of the swamp environment and a shift back to bottomland forest.

The relationship of the Swamp pollen peak in the Whiskey Creek pollen diagram to the sedimentary record raises some interesting questions regarding the use of sedimentary data in paleoecological reconstruction. The Upper and Lower Lignite Series represent the two principal periods in Whiskey Creek time where direct sedimentary evidence exists for the presence of peat swamps. Yet the Swamp pollen profile indicates that during the period where the sampling site was accumulating peat, the overall level of Swamp pollen was comparatively low. Only later in time, when the sampling site was accumulating mud (that represents the overlying shales now termed the Valley Plant Beds), does the Swamp pollen level rise to a peak in excess of 30%. Although most Swamp pollen peaks in the study sections are of smaller magnitude than the Whiskey Creek example, it is quite common to find that a Swamp peak does not always correlate to the same level in a section where one finds the best lignite development. The presence of lignites is clearly not *prima facie* evidence of maximum extent of swamp development as evidenced by these pollen records of the Swamp Paleoassociation in the Succor Creek area.

In excess of 95% of the pollen of the Swamp Paleoassociation is that of the Taxodiaceae, either *Glyptostrobus* or *Taxodium*. There can be little doubt that both plants were intimately associated with environments where peat was accumulating. The Rocky Ford section has excellent leaf impressions of *Glyptostrobus* and some *Taxodium*. An organic zone at the Devils Gate section (Fig. 1, loc. 9) is dominated by leaves and branches of *Glyptostrobus*. Virtually all preserved fossil stumps in the Succor Creek area are rooted in lignites or organic shales and invariably are assignable to the Taxodiaceae, based on thin-sections of the wood. An excellent "fossil forest" of this type is present in the upper Rockville section.

Lack of correlation between Swamp pollen peaks and organic deposition is rather surprising but an explanation may be found in the nature and extent of the Succor Creek swamps. Given the variable topography assumed for the landscape, the most likely site for swamp development would be shallow lake margins and headwaters. It is possible that most of these swamps were of limited geographic extent and rather patchily distributed over the landscape, based on the relatively minor contribution of Swamp pollen to most pollen spectra. In the case of the Whiskey Creek lignites, although peats were accumulating at the sample site, the swamp was too small for the input of Swamp pollen to override the massive pollen influx from the surrounding broad-leaved and coniferous forests.

The presence of lacustrine shales of the Valley Plant Beds overlying the lignite indicates a probable increase in lake level, which converted the old swamp to an open-water site where mud accumulated over the peat. The cause of such an increase in water level is conjectural but the overall Whiskey Creek floristic

record shows no evidence of profound disturbance by volcanic activity, so ash fall or lava dams are unlikely. However, an earthquake induced landslide could have dammed the valley, increased the water level (Adams, 1981) and formed an open-water environment at the sampling sites. The surrounding areas, previously supporting bottomland forest elements, would have become flooded and more extensive areas of swamp could have spread around the expanded lake margin. In this case, the increased area of swamp development resulted in larger inputs of Swamp pollen and hence the pollen peak in the Valley Plant Beds. Lignites and other organic sediments in interior continental deposits certainly record the presence of swamps but, in any specific section, they need not signify the period of maximum swamp development in the region as a whole.

SHIFTS IN COMMUNITY DISTRIBUTION

A major dynamic feature of the pollen diagrams of the Whiskey Creek, lower Rockville, and lower Shortcut sections is the interaction in relative frequency of the Bottomland/Slope and Montane Conifer Paleoassociations. These pronounced oscillations raise two primary questions: to what extent did mutual oscillations occur in the major components of the source vegetation, and what mechanisms exist to explain changes in the nature of the source communities?

Our Succor Creek pollen data are tabulated as relative frequency pollen diagrams made up of individual pollen spectra, each spectrum representing the total pollen tabulated for a sample. Within each spectrum the contribution of each taxon is expressed as a percentage of the total pollen count for that sample (Taggart & Cross, 1974). The paleoassociation percentages simply represent the aggregate of percentages for all taxa assigned to a specific paleoassociation. Essentially the paleoassociation curves constructed from these percentages are analogous to curves for individual taxa although they tend to be highly damped because each paleoassociation contains more than a single taxon. This damping is particularly true in the case of the Bottomland/Slope Paleoassociation since it is the most inclusive of the categories. The primary limitation of a relative pollen diagram is that if there is a major shift in the pollen contribution of any major component of the spectrum the relative frequency of the remaining components must change, since all data are expressed as a percentage of total pollen. The result may be a change in the expressed percentage of some components of a spectrum without changes in the importance or distribution of the source plants.

Such an anomalous interaction is most likely to occur in the case of a genus such as *Pinus*, which produces disproportionately large quantities of pollen with excellent aerodynamic and hydrodynamic characteristics for dispersal and high durability. Pine may be present as trees sparsely scattered in a forest, yet may represent 10% of the pollen record. For illustration, let us assume that the remaining 90% of the pollen rain is made up equally of the Bottomland/Slope and Montane Conifer Paleoassociations, each contributing 45%. Due to some circumstance, the percentage of pine pollen might increase to 20%. This could be due to a number of factors, a slight increase in population levels of pine, establishment of even a few trees somewhat closer to the basin, etc. None of these factors need imply any significant increased importance in the contribution of pine in the local

vegetation and the composition and distribution of other forest elements would remain essentially unchanged, yet the Bottomland/Slope and Montane Conifer pollen levels would each drop to 40% due to the greater input of pine pollen. It should be noted, however, that although the drop in the other paleoassociation percentages is meaningless "noise" relative to their composition and distribution, the increase in the level of pine pollen does reflect some real event relative to pine populations or distribution even though it might be marginally resolvable in terms of regional phytosociology.

A similar situation occurs with alder pollen in some samples. *Alnus* probably occurred in thickets marginal to ponds, lakes, and wetlands and, when the plants were abundant locally, their pollen may have dominated a specific spectrum, enhancing the Bottomland/Slope percentage at the expense of other paleoassociations. Such single taxon biases are usually apparent and their effect may be mitigated by excluding the suspect taxon from the pollen sum when assessing the dynamics of the remaining components.

In spite of all such considerations, the Whiskey Creek, lower Rockville, and lower Shortcut sections are characterized by pronounced oscillations or shifts between the Bottomland/Slope and Montane Conifer Paleoassociations. Such oscillations are not single taxon phenomena but represent coordinated shifts in the representation of entire paleoassociations, which are, by their nature, damped due to the inclusion of multiple taxa. Although it may be argued that the relative response of the individual paleoassociations is linked, due to the nature of relative pollen diagrams, such a view overlooks essential realities in the nature of plant community distribution. Climax or subclimax forest communities are essentially exploitive, occupying all sites within the biotic and abiotic tolerance ranges of their constituent species. An increase in the absolute input of Montane Conifer pollen must result in a decrease in the percentage of Bottomland/Slope pollen, based on the nature of relative pollen diagrams, but this interaction simply mirrors real changes in the source vegetation.

An increase in the absolute influx of the Montane Conifer assemblage must be the result of an increase in the area of the source vegetation, or an increase in relative population, or increasing proximity to the basin. Such an increase in pollen must be at the expense of reduced distribution or a relatively reduced population for some other components of the forest. Because Swamp and Xeric Paleocommunities produce pollen at relatively low levels, and pine is only background "noise" in most samples, it follows that the forest unit that must have been displaced was some component of the Bottomland/Slope assemblage. Similar arguments hold for decreases in the absolute input of the Montane Conifer assemblage or increases or decreases in the absolute pollen input from the Bottomland/Slope Paleoassociation. Relative pollen diagrams certainly have pitfalls that must be avoided, but when interactions involve highly damped co-dominants in an assemblage, one can be confident that the relative frequency data are reflecting real changes in vegetation distribution.

The most obvious causal agent for such oscillation is climate, e.g., cooler conditions favoring the Montane element at the expense of the Bottomland element with the converse true in the case of a warming trend. The crucial questions

then become: what was the magnitude of the thermal oscillation and over what time period did it operate?

Time Factors

Generally the time period represented by a specific section must be deduced, since direct dating techniques lack adequate resolution. Two approaches suggest themselves: estimates based on relative sedimentary rates and estimates based on biological phenomena within the sequence in question. Although both procedures lack both precision and accuracy, there is evidence that they both converge on time spans in the order of magnitude of thousands to tens of thousands of years for most sections studied in the Miocene of the Succor Creek area. Transport and sedimentation of volcanic detritus is episodic and rates are clearly influenced by the magnitude of the eruptions and the distance and orientation of the basin from the outpouring of material relative to available modes of transport (gravity, ejection force, wind, and water). Unless a basin is quite close to the volcanic source or directly downwind, direct ash fall may be a relatively minor source of sediment. However, reworking of great quantities of ash by water transport from an extensive watershed will concentrate great quantities of ash in fluvial valleys and lacustrine basins. Unfortunately, little information is apparently available on the rates of sedimentation under such conditions.

Much more data are available for more conventional detrital sedimentation (Schindel, 1980; Spicer, 1981) although the applicability of such data may be limited for many of the Tertiary floras of the Pacific Northwest. Schindel (1980) discussed sedimentary rates extensively in an attempt to demonstrate that many biological phenomena, particularly in the context of community ecology, occur at time scales below the limits of resolution attainable by common paleoecological sampling procedures. An uncritical analysis of Schindel's conclusions might indicate that it is pointless to search for small-scale community phenomena in the fossil record of terrestrial systems. While it is not our intention to speculate as to the validity of Schindel's conclusions relative to marine studies, the success of Quaternary pollen analysis in documenting postglacial vegetation dynamics represents a *prima facie* case that the conclusions are not valid for all terrestrial systems.

If the study sections in the Succor Creek area represent very long periods of time (10^5 to 10^6 years), it follows that limited numbers of productive pollen samples are inadequate to yield useful resolution in documenting patterns of vegetation dynamics. In contrast, should the time scale represented by the sections be roughly comparable to those encountered in postglacial pollen analysis (thousands to a few tens of thousands of years), pollen analytical techniques should prove as productive in those Tertiary deposits as they have in postglacial studies. We propose that the latter situation pertains to the sections we have studied of the Succor Creek, and that the question is critical enough to present here sedimentary evidence in support of our position. The analysis has three components: the relative time periods represented by rocks accumulated under different sedimentary environments, the reasonable range of absolute time values applicable for the study sections, and the relative and absolute resolution attainable, given the productive pollen samples available.

Relative Time Equivalents of Various Rock Types.—Inland continental deposits usually exemplify two primary depositional environments, fluvial deposition in streams and rivers and lacustrine deposition in ponds and lakes. Although deposition of normal detrital sediments can be assumed to have occurred in the Succor Creek area, the bulk of the clastic material making up the Sucker Creek Formation is derived from variously altered, size-sorted, water-transported volcanic ash. Although direct ash-falls can be noted in most sections, most of the detrital pyroclastics have largely been reworked following ash falls on the Succor Creek watershed(s) with concentration of sediment in the depositional basins. Fluvial sedimentation appears to dominate through the formation as a whole (Kittleman et al., 1965), and this is certainly the case in our individual study sections. Some gravel conglomerates are known, but most fluvial deposits consist of coarse to fine-grained arkosic sands and silts. Lacustrine sediments are typically more limited in exposure and occurrence and range from relatively well-sorted shales and siltstones, through increasingly organic mudstones and siltstones, to impure lignites. The coarse-grained fluvial sediments generally accumulate more quickly than the fine-grained sediments of lacustrine systems so that a given thickness of fluvial sediment represents a shorter period of time than does an equivalent thickness of lacustrine deposit. Although both fluvial and lacustrine sediments typically have differential sedimentary rates within their own category, usually correlated with grain size, it is instructive to compare the generalized sedimentary rates for fluvial systems with those of lacustrine environments, in order to compare the relative time spans represented by the two major depositional environments in each study section.

Schindel (1980) compiled measured or inferred sedimentary rates for 15 fluvial and 29 lacustrine environments. The fluvial systems had a mean rate of 86,000 Bubnoff units per year (1 B equals 1×10^{-6} m/year) while lacustrine rates averaged 5,800 B/year. The ratio of mean fluvial to mean lacustrine rates is 14.83, implying that the average fluvial deposition rate is approximately 15 times faster then the mean for lacustrine environments. Although no exact value for relative sedimentary rates can be given, it is instructive to apply the ratio of these means, based on Schindel's compilation, to both the Whiskey Creek (Fig. 4) and Type sections (Figs. 8, 10). The Whiskey Creek section consists of approximately 102 m of sediment with the basal 53 m (52%) representing largely fluvial sands and the upper 49 m (48%) comprised of lacustrine deposits. The Type section represents 208 m of sediment, excluding the 11 m Rocky Ford sequence, of which approximately 170 m is fluvial (83%) and only 34 m (17%) is lacustrine. If we arbitrarily expand the lacustrine units by a factor of 15, followed by a uniform reduction of the entire sequence to produce a display scaled to the original section diagram, we obtain the time-corrected sedimentary plots included in Figs. 4–8. Although lacustrine sediments comprise only 48% of the measured Whiskey Creek section, they account for over 91% of the depositional time interval, assuming the 15-fold correction factor for differential sedimentary rate and no significant diastems in the sequence. Similarly, lacustrine sediments in the Type section represent only 17% of the section yet comprise 75% of the depositional time interval. Obviously such figures will shift with the differential rate factor, but lacustrine units will always represent a more significant portion of the entire

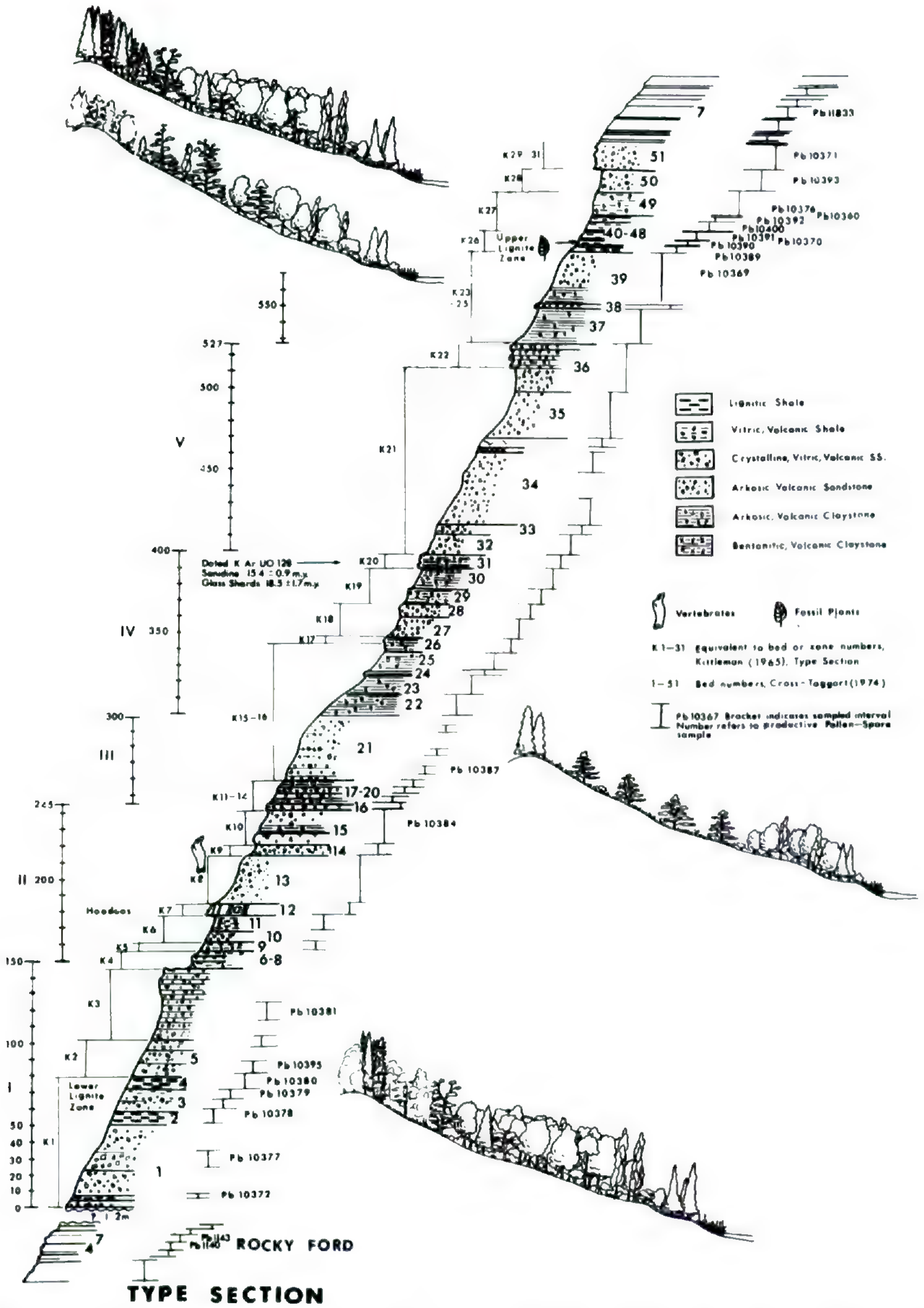


FIGURE 10. Sedimentary sequence for the Type section showing the rock units as recognized by Kittleman et al. (1965), on the left side of the diagram (K1–K31), and the intervals we recognized when remeasuring the section during the 1974 field season, indicated by the numbers immediately to the right of the section display. A sequence of units above Unit 51 was measured and sampled in 1977. The scale on the far left side of the diagram records the cumulative thickness of the section in feet. The bracketed areas on the right side of the display indicate the position and thickness of units sampled for palynological analysis. The Pb numbers indicate the position of productive pollen and spore samples that are included in Figure 8. Our Unit 13 (K8 of Kittleman) contains vertebrate fossil material while the shale sequence represented by Units 40–48 (K26 of Kittleman) is an excellent plant macrofossil zone. Generalized vegetation reconstructions are included that show the sequence of inferred vegetation development through Type section time based on the pollen data in Figure 8. Note that the pre-disturbance vegetation at the base of the section differs from the typical "climax" forest for the region due to the relative absence of the Montane Conifer Paleoassociation, probably caused by slightly warmer temperatures in early Type section time.

sedimentary time interval than their thickness, relative to fluvial sediments, would imply.

Sampling Resolution.—This relationship of relative time interval impacts the time resolution provided by productive pollen and spore samples as well as the representation of leaves and other macrofossils. All lithologicaly identifiable sedimentary units in a section are sampled at least once and often several times. A total of only 13 of 70 samples from the Type section yielded sufficiently good recovery of fossil pollen and spores to justify quantitative analysis. The recovery rate of palynomorphs from coarse sediments, such as arkosic sands, is usually quite low. This is probably related to several factors, including increased opportunity for oxidation in coarse sediments and dilution of the pollen content due to rate of accumulation of sediment during seasonal periods when pollen levels are low. Post-depositional destruction of pollen and spores may also be a factor, a matter discussed under "Sedimentation and Alteration of Succor Creek Rocks."

The pollen recovery pattern for the Type section indicates a clustering of productive samples in the lacustrine sediments at the base and top of the section. Without consideration of the impact of differential sedimentation rates for fluvial and lacustrine sediments it would appear that a great stretch of time in the center of the section is undocumented. In point of fact, the generally satisfactory yield of samples from lacustrine sediments is sufficient to document most of the time interval represented by the section.

Absolute Depositional Intervals.—Conventional radiometric dating cannot be expected to yield data on the time interval represented by sections. Error values for single dates typically exceed 100,000 years and correspondence between dates is even less precise. Kittleman (pers. comm., 8 May 1974; 9 March 1978) cited two dates from coexisting glass shards and sanidine from a single sample from the Type section that differ by approximately three million years. While much of the differential is probably due to rapid gas migration from the sanidine, this underscores the limitations of radiometric techniques in attempting to resolve relatively short time spans in older rocks. Some varved lacustrine sediments are found in the Sucker Creek Formation but their occurrence and extent within the four study sections is too limited to provide direct sedimentary calibration.

It is instructive to apply the previously calculated mean value for fluvial and lacustrine systems to the study sections. The fluvial value of 86,000 B/yr translates to approximately 12 years for the accumulation of a meter of sediment (0.086 m/yr) while the 5,800 B/yr lacustrine value represents approximately 172 years for a meter of sediment (.0058 m/yr). In the Whiskey Creek section the 53 m basal fluvial unit would thus represent 636 years of accumulation and the upper 49 m lacustrine unit would represent 8,429 years for a total depositional period of 9,064 or slightly less than 10,000 years. In the case of the Type section, 170 m of fluvial deposits would represent 2,040 years while the 34 m of lacustrine deposits would represent 5,848 years for a total interval of 7,888 years. In this type of calculation, a major consideration, not fully taken into account in Schindel's (1980) values for rate of accumulation of sediments in different environments, is the number and magnitude of gaps in the record. We recognize the possibility, even probability, that some diastems and possibly some unconformities (where an unknown increment of previously sedimented deposits may have been removed) may exist in our sections. Recently, Sadler (1981, p. 583) noted this potential weakness in

Schindel's "constancy of sedimentation" factor, but did allow that in thinner stratigraphic sequences the determination of rates of sedimentation, where no erosion intervals are evident, probably is useful. In the sections of the Sucker Creek Formation, the continuity of the apparent paleosuccessional communities and lake beds provide some evidence that we are considering stratigraphic accumulations with only minor diastems and unconformities.

Rates of accumulation used in the previous examples are conservative when compared with the estimate of Dorf (1960), determined through a different line of reasoning, of 5.5 yr/m (.183 m/yr) for the deposition of the 365 m of pyroclastic sediments in the "fossil forest" section of Amethyst Mountain in Yellowstone National Park. McLeroy and Anderson (1966) concluded that the 15 m of lacustrine sediments accumulated in Oligocene Lake Florissant (Colorado) represented a period of 2,500–5,000 years. This estimate was based on the proportions of various types of varved laminae representing diatomite-sapropel (1 mm/yr), graded beds (8 mm/yr), and pumice laminae (1.5 cm/yr). The lacustrine sediments of our sections are comprised of rocks primarily of the graded and pumice laminae type. Assuming that the two types were equally represented, McLeroy and Anderson's values would result in a rate of 1.2 cm/yr or 90 yr/m. This rate is almost twice that of the 172 yr/m used in the examples above.

The function of this exercise is to provide a range of possible values to evaluate, in the light of other criteria, not to precisely calibrate the sections, for there are far too many variables to make that possible. Two significant points emerge. First, the absolute thickness of any section relative to the other is not a reliable guide to estimate the time that each section represents. The Whiskey Creek section, with 49 meters of lacustrine sediments, probably represents more time than the Type section, which, although twice as thick, has only 34 meters of lacustrine sediments. Second, and perhaps more important, the time periods indicated for such rock units are in the order of thousands to tens of thousands of years. If sedimentation was an order of magnitude faster we would be dealing in only centuries, while we might have to consider as much as 100,000 years, if sedimentary rates were an order of magnitude slower. Extremely slow sedimentation seems unlikely since availability of relatively unconsolidated ash could be expected to result in very rapid accumulations of thick bodies of water-transported ash sediments in the topographic lows. Although ash availability was episodic, it was probably superabundant when available, as witness the rapid ash blockage of the Toutle River in Washington with the eruption of Mt. St. Helens (Rosenfeld, 1980, p. 504).

The paleobiological data from the pollen spectra seem generally in accord with the order of magnitude implied by this rough attempt at calibration. The basal fluvial sand at the Whiskey Creek section represents 636 years at the 86,000 B/year rate and this value may be conservative. A clay shale immediately below the fluvial unit, a calcareous ironstone approximately half-way up the unit, and a shale overlying the sand, all yielded essentially similar pollen spectra. It is probable that the source vegetation was essentially the same in each of the three cases, implying that little time elapsed during the accumulation of the basal sand. Similarly, the swamp interval documented in the upper Whiskey Creek section would have required between 2,000 and 4,000 years based on the calculated value

of approximately 8,400 years for the lacustrine unit. Such a value is not unreasonable for hydrologic succession in a modest-sized lake and, if in error, is perhaps on the long side.

In summary, the exposed stratigraphic sections in the Succor Creek area appear to represent geologically short time intervals (several thousand to several tens of thousands of years) within the one to two million year span of Sucker Creek time. Although much of Sucker Creek interval is probably undocumented by continuous sedimentation, each study section represents a time period wherein we might expect to discern vegetation dynamics in forest communities.

Climax Vegetation Dynamics

The fluctuations in the relative importance of the Montane Conifer and Bottomland/Slope Paleoassociations probably occur over intervals ranging from several centuries to a few thousand years. If this is the case, it would argue for relatively small temperature fluctuations. The mosaic of Succor Creek forest communities may well have represented a relatively delicate distributional equilibrium in response to the then-current mean annual temperature and annual range of temperature. Slight shifts in either parameter over a period of centuries would result in a redistribution of the community mosaic. No evidence exists for extreme topographic relief in the area during Sucker Creek time and if we assume the vegetation to have been developed on low-slope gradients, such gradients would amplify the effect of slight elevational shifts in ecotones, greatly increasing the area of one forest type relative to the other and greatly increasing or decreasing the distance that pollen might have to be transported. Small thermal oscillations thus appear sufficient to account for the observed shifts in the relative importance of the Bottomland/Slope and Montane Conifer Paleoassociations. These thermal oscillations will be discussed later in the context of cliseral succession.

POST-DISTURBANCE SUCCESSION

Volcanic Disturbance

The most dramatic feature of the pollen profiles of the Rockville, Shortcut, and Type sections is an abrupt change in the composition of the pollen flora at some stratigraphic level in each of the sections sampled. In each section the transition is marked by a significant decrease in the frequency and diversity of the Bottomland/Slope Paleoassociations with an increase in the importance of the Xeric Paleoassociation and a complex of "Other" pollen representing angiospermous plants of unknown taxonomic affinities. The Montane Conifer Paleoassociation is an important element in the lower Rockville and Shortcut sections. At the transition point in these two sections, the pollen of the Montane Conifer complex declines to insignificance, concomitant with the decline of the Bottomland/Slope element. It is not represented at the base of the Type section but is represented in significant amounts in the nearby Rocky Ford section which is of uncertain stratigraphic position

We described this phenomenon and suggested that the shift of dominance from one type of vegetation to another, as shown in pollen diagrams (Taggart & Cross, 1974, figs. 2 and 3), might be related to a secondary succession initiated

by volcanic disturbance of the forest vegetation or a cliseral succession due to a pivotal change in regional climate. With the accumulation of additional data from the Type section, where the pollen diagram indicates the eventual return of diverse forest vegetation, the succession hypothesis was greatly strengthened. We have discussed this concept in detail in a recent paper (Taggart & Cross, 1980). On a time scale measured in thousands of years, the forest habitat in the Succor Creek area was clearly unstable. It was subjected intermittently to various types of volcanic catastrophes: direct ash falls of considerable thickness, ash flows of high temperature and velocity, blast effects of violent explosions, the poisonous effects associated with gas venting, mudslides that commonly accompany major volcanic activity near the source, and damming by flows and sediment choking of valleys causing extensive muddy lakes. Tertiary paleobotanists have considered the mechanical effect of ash falls and the lethal effects of gas venting in facilitating leaf fall, but most, with exceptions such as Dorf, in his studies of the Eocene "fossil forests" of Yellowstone National Park (1960, 1964) and Axelrod (1968, p. 720), have not considered the impact of regional volcanism on forest vegetation dynamics. The Yellowstone sequence clearly indicates that ash falls, mud flows (lahars), and fluvially transported ash accumulations periodically buried existing forests, and these, acting together with accompanying noxious gases and occasional explosive forces, probably destroyed all vegetation especially at the sites of the deposition of thicker ash layers. We have suggested that the abrupt decline in the number and diversity of Bottomland/Slope elements in the Rockville, Shortcut, and Type sections and a concomitant decline in the Montane Conifer element at Rockville and Shortcut, represent incidents of intermittent destruction of extensive areas of the forest vegetation in the Miocene of the Succor Creek region. The magnitude of areas stripped of vegetation would have varied with the duration and size of the volcanic outbursts.

When extensive disruption of Succor Creek vegetation by volcanic activity was first proposed as a hypothesis to explain the sudden transitions in the Rockville, Shortcut and Type section pollen diagrams (Taggart, 1971; Taggart & Cross, 1974, 1980) such a reconstruction might well have been considered extreme. But the explosive eruption of Mt. St. Helens on 18 May 1980 provides a graphic example of the effect of local volcanic activity on diverse forest vegetation. Rosenfeld (1980) gives a wealth of interesting observations regarding the effect of this eruption on surrounding communities. He noted that near the breached north side of the mountain (in background of Fig. 12) nearly every slope exposed to the blast within 10 km was denuded of vegetation and covered with ash and to 15 km, trees were stripped of their branches and snapped off at their bases. Trees

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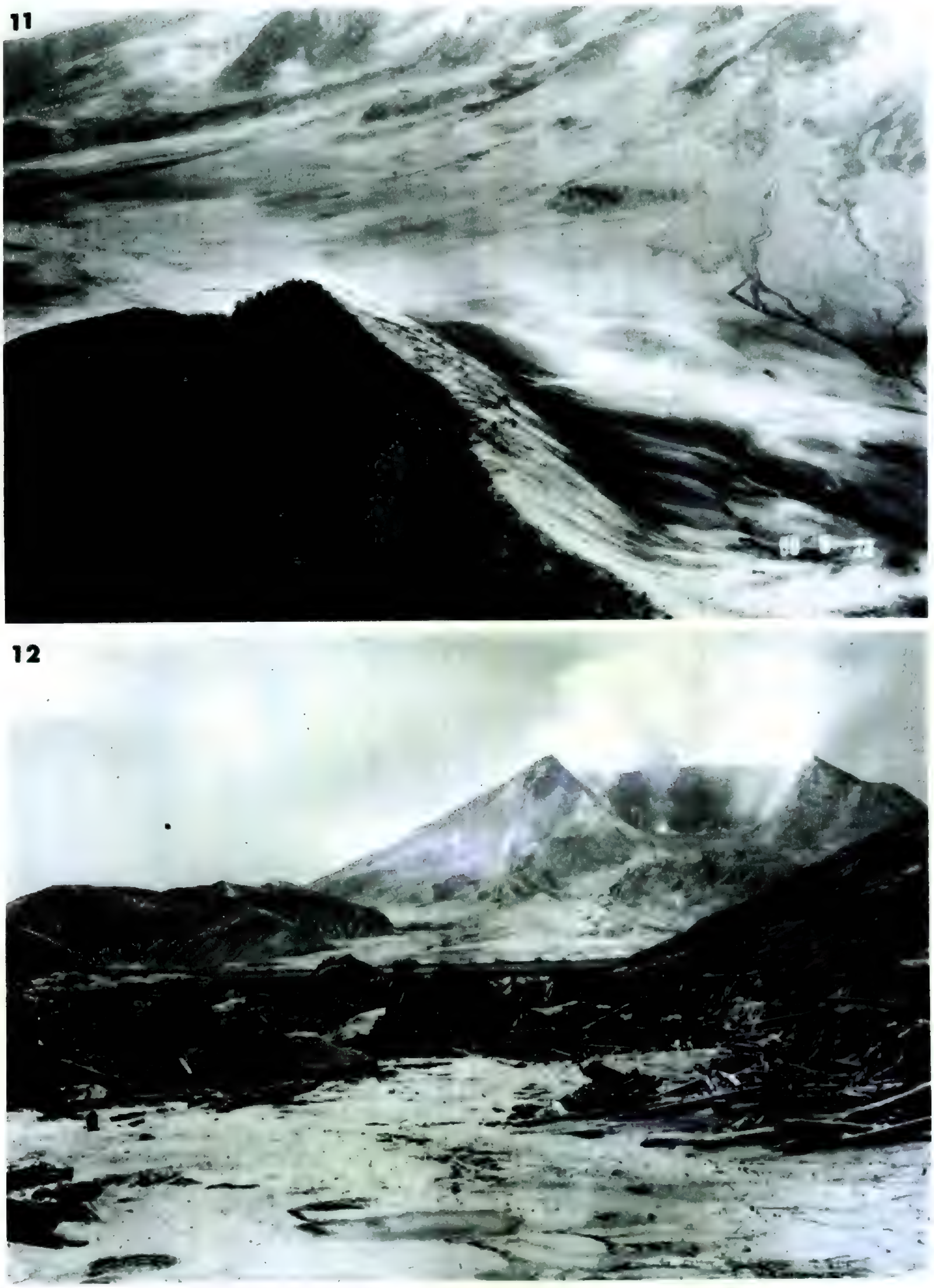
FIGURES 11–12.—11. A ridge north of the Toutle valley showing the directional effects of the blast accompanying the 18 May 1980 eruption of Mt. St. Helens in southwestern Washington. The right side of the ridge in this photo, facing the blast, was scoured of vegetation and blanketed with ash. The forest on the lee (left) side of the ridge suffered less disruption with singeing and burning of leaves, stripping of branches, and felling of some trees. (This photo, provided by Charles L. Rosenfeld, was originally published in Rosenfeld, 1980, Amer. Sci. 68: 500.)—12. The northwest shore of Spirit Lake, with Mt. St. Helens in the background, following the 18 May 1980 eruption. The blast,



projected directly from the volcano some 10 km distant, hurled blocks of rock over 20 m in diameter into this area. Blast forces and the downward thrust of mud and other debris into the far side of the lake pushed a wall of lake water northward, scouring slopes up to 300 m above the original lake level. The mud and log-strewn landscape in the foreground represents the aftermath of this surge. (This photograph, provided by Charles L. Rosenfeld, was originally published in Rosenfeld, 1980, Amer. Sci. 68: 501.)

on lee slopes were left standing but their leaves were singed or burned (Fig. 11). The force of the blast and displacement of debris forced the waters of Spirit Lake 300 m up the slope of Mt. Margaret, effectively denuding that area of vegetation cover (Fig. 12). Landslides and debris-flow scoured hillsides, removing more than a meter of soil in many areas. Ancillary effects of the blast include the creation of impounded lakes in tributary valleys unaffected by the primary blast, the possibility of high sediment yields and additional mudflows with the re-establishment of drainage channels, and the extreme erosional instability of slopes denuded of vegetation cover. In lowland areas, the ash, compacting underlying organic debris, has created a mosaic of depressions that are already acting as small depositional basins. As impressive as the eruption of Mt. St. Helens was, it is insignificant relative to the magnitude of the events leading to the massive pyroclastic Tertiary plateaus of the Pacific Northwest. In referring to such deposits, Heiken (1979) suggested, ". . . Such eruptions would be awesome, burying hundreds of thousands of km^2 under pyroclastic flows that move away from the vent at hurricane velocities. Eruption clouds may deposit fallout over millions of km^2. A safe distance from which to watch such an event might be the earth orbit of a space station . . . ."

While our interpretation of the Rockville, Shortcut, and Type sections assumes catastrophic destruction of forest vegetation, we may in fact be understating the magnitude of disturbance. Where sufficient ash exists to preserve a flora or fauna, it is quite reasonable to expect a discontinuity or change in the plant or animal record signifying a community disruption.

The events following widespread destruction or disruption of a forest community depend on the areal extent and magnitude of the damage, and the biotic potential of the region. In an extant biota, many species exist that are adapted to colonizing or pioneering strategies. Such species will exploit open, often drier, habitats, sometimes leading to the establishment of a secondary succession in which the post-disturbance area is initially dominated by forbs and grasses. Under a mesic climatic regime trees and shrubs will seed into the area, either from seed pools in the soil or by dispersal from relict areas or undisturbed peripheral communities. Thus a period of forb dominance is usually succeeded by a shrub stage, followed, barring further disturbance, by the gradual re-establishment of a forest system. Such a succession requires a considerable range of ecological diversity in the regional flora, including the pioneer species characterizing the early seral stages.

The Eocene Yellowstone biota may well have lacked the diversity for a distinctive early successional sequence. Megafossil studies by Dorf (1960, 1964) and pollen analysis by Fisk (1976) indicate that recovery consisted of the recolonization of the area by essentially the same species that constituted the pre-disturbance forest. This is not surprising because herbaceous dicots, grasses, and even many shrubs apparently are poorly represented in the Eocene (Leopold, 1969, p. 382). It is these groups of plants that characterize the earlier stages of the distinctive successions that can be documented for extant floras.

By mid-Miocene time, however, such plants had undergone considerable evolution. In the Succor Creek, herbaceous dicots (Chenopodiaceae, Amaranthaceae, Compositae, Malvaceae, Onagraceae), grasses (Gramineae), and woody

shrubs, are well-represented (Graham, 1965; Taggart, 1971, 1973; Taggart & Cross 1980). The pollen record appears to indicate a role for such plants in distinctive post-disturbance succession. A recently ash-covered landscape is inherently edaphically dry (Bowman, 1911, pp. 203–205; Leopold & MacGinitie, 1972, p. 174) and, even in areas of abundant rainfall, such a surface generally does not represent a suitable seed-bed for the re-establishment of forest trees. Such habitats are within the adaptive range of exploitation by numerous herbaceous species. The peaks in the pollen profiles representing the Xeric Paleoassociation (principally Compositae, Gramineae, Chenopodiaceae/Amaranthaceae, and Malvaceae), which appear following the disturbance transitions at the Rockville, Shortcut, and Type localities, indicate initial colonization of the ash-covered landscape by these taxa (Fig. 9-I). Although a variety of shrub and tree species may have begun seeding into the area during the post-disturbance herbaceous stage, the most consistent feature, best documented at Rockville, is a rise in the level of pine pollen, indicating the development of a pine-stage later in the successional sequence. Pine pollen is at about 10% in the samples of sediment deposited immediately before or shortly after the disturbance, which is essentially the level of pine in the regional "background." However, the relative frequency of pine rises to 69% at the top of the Rockville section. Post-disturbance levels of pine reach about 30% in the Shortcut locality and 45% in the Type section. Although such levels are not sufficiently high to suggest a closed-canopy pine forest (Leopold, 1964), they do suggest an open, second-growth pine assemblage that may have provided shelter for establishment of seedlings of more shade-tolerant forest species (Fig. 9-II). Whereas the Rockville record ends with this "pine stage," the Type section record continues on to later stages and indicates that sweetgum (*Liquidambar*) and hickory (*Carya*) may have been significant components in the post-pine reforestation continuum (Fig. 9-III).

Although the immediate post-disturbance pollen record for the Bottomland/Slope element is low in diversity and in importance, it does persist. The pollen record indicates a limited riparian assemblage consisting of relict forest remnants or species that were able to become re-established relatively rapidly on the more mesic sites near lakes and streams. The Bottomland/Slope community diversity averages 19 taxa per sample, while the two post-disturbance samples average only 6 taxa. Oak, willow, and sycamore are the most prominent components of this riparian thicket.

The uppermost series of samples from the Type section record the return of forest vegetation, including both the Bottomland/Slope and Montane Conifer elements with diversity ranges comparable to the forest records throughout the study area (Fig. 9-IV). It is possible however that the Bottomland/Slope forest component of the upper Type section may be sub-climax in nature since it is dominated by oak in contrast to the elm dominance characteristic of the Whiskey Creek, lower Rockville and Shortcut, and lower Type sections. The megafossil record for this forest includes *Ulmus*, *Zelkova*, *Populus*, *Salix*, and *Carya*.

Objections to the Succession Hypothesis

Paleobotanists have documented cliseral succession in the Tertiary of the Pacific Northwest, both regionally (Chaney & Axelrod, 1959) and locally (Shah,

1968; Smiley et al., 1975b), but our Succor Creek Flora studies may represent one of the first attempts to document post-disturbance succession (primary or secondary) in a Tertiary flora. It is reasonable to ask why such processes have not been identified previously, or if alternative explanations might provide a better interpretation of the data we have presented. We will briefly discuss some issues that may bear on these questions.

Limited Resolution.—The research of Schindel, 1980, would suggest that the recognition of processes such as succession is beyond the range of resolution in conventional paleobiological studies due to the duration of the process relative to the rate of sedimentation. In point of fact, Quaternary pollen analysis of bogs and lakes has proven successful in documenting both secondary and cliseral succession using sampling of variable intensity. The accumulation of lake muds and peat is a slow process with a high constancy factor, in the terms of Schindel (1980). The remarkable Clarkia Lake Beds, now under intensive study by Dr. Jack Smiley, University of Idaho, and others (Smiley et al., 1975a; Smiley & Rember, 1979, 1981; Rember & Smiley, 1979; Niklas & Brown, 1981; Giannasi & Niklas, 1981; Smiley & Huggins, 1981; Lewis, in press), is a Miocene deposit (est. age 20 m.y.) of slightly more than eight meter thickness of thinly-laminated lake beds containing remarkably preserved leaves, fruits, seeds, flowers, pollen and spores, algae, and several types of fauna. This is a prime example of a fossil flora showing continuous changes in plant community structure in an identifiable unit of time, possibly several centuries. Another example of fine stratigraphic and temporal resolution possible, is the landmark study of Zangerl and Richardson (1963) on the Mecca Quarry Shale Member of the Linton Formation (Pennsylvanian) of Indiana. There, the resolution of the biotic changes and sediment deposition were recorded and amply documented as a year-by-year series of events for a depositional period of less than five years. This finely-laminated black shale was nearshore black mud deposited in very shallow water of a transgressing sea. Detailed stratigraphic palynology of a flora, such as the Succor Creek, is merely the logical extension of the use of a proven analytical tool.

In the Whiskey Creek lignite beds, sampling was made at intervals comparable to those employed for Quaternary pollen analysis, but the results obtained indicate no new patterns of interaction. The Upper Lignite Series diagram (Fig. 5) indicates a pattern of mutual oscillation between Montane Conifer and Bottomland/Slope elements, similar to that seen in the main section (Fig. 4). The pattern of increasing Swamp pollen levels in the Upper Lignite Series is consistent with the trend in the section as a whole and there is generally a satisfactory "fit" between the pollen levels in the uppermost samples from the Upper Lignite Series and the overlying shales, as documented in the main Whiskey Creek pollen diagram. The fit between the main section diagram and the lowermost Upper Lignite samples is quite poor however and may indicate the effects of limited resolution in the main section diagram. The transition back to high levels of Montane Conifers, as indicated in the basal samples from the Upper Lignite Series, occurs in approximately 1.5 meters of strata and is comparatively abrupt when compared with most such shifts noted in either the main Whiskey Creek section (Fig. 4) or the Upper Lignite Series diagram (Fig. 5). It is possible that the shale-lignite transition represents a diastem of unknown duration or the abrupt change in

pollen levels may signify a relatively rapid return of well-developed conifer forest in the area. The 1.5 meters of intervening section would represent a period of approximately 300 years using the criteria previously discussed so it is possible that the transition may mark a shift of community types requiring only a few centuries for completion. Detailed sampling through the shale unit and into the Upper Lignite Series would be required to resolve the question.

Whether fortuitously or by some design, virtually all of the successional events in our sections occur in coarse sediments with higher rates of sedimentation, which may indicate diastems or times of rejuvenation of erosion cycle. Even the limited productivity of such samples is sufficient to identify the presence of the process.

Lack of Previous Recognition.—Recognition of the occurrence of a post-disturbance succession at several sites in the Succor Creek area is possible only because we have undertaken detailed pollen analysis with very close stratigraphic control. Palynology is an ideal tool for documenting some types of events that occurred during the time-frame represented by sediments, even though those events may have occurred at sites or in regions at some distance from the basin of deposition. This is particularly true for herbaceous plants, which are usually poorly constructed for efficient representation. Quaternary pollen analysis is conducted with high sample density to record such phenomena and they can be and are distinguished. Most conventional stratigraphic palynology studies of Tertiary rocks are conducted to establish regional correlations of larger stratigraphic units (formations, members, etc.) and thus lack the resolution necessary to recognize temporally restricted phenomena such as secondary succession. Conventional Tertiary paleobotany in the Pacific Northwest primarily has involved evaluation of macrofossils and most of the classic studies lack detailed stratigraphic control. Axelrod (1968, p. 720, footnote 2) states that paleosuccessional stages following destruction of forests by ash-falls or fire have been identified in association with four fossil floras; two Eocene, Bull Run (Nevada) and Germer Basin (Idaho), and two Miocene, Carson Pass (California) and Purple Mountain (Nevada).

The most likely recognition feature for a successional community in the macrofossil record would be a low diversity florule. Taggart and Cross (1980) have indicated that low diversity florules in the Succor Creek (dominated by willow, oak, and sycamore) correlate closely with the successional intervals indicated in the pollen stratigraphy. One must have adequate stratigraphic information to rank florules as to time of occurrence and it is unlikely that the significance of even the low-diversity Succor Creek florules would have been appreciated without the framework provided by detailed stratigraphic correlations and concurrent pollen studies.

Finally, no matter how detailed the information available for a time sequence, disturbance that initiates succession must occur within the period of time represented by the sedimentary sequence studied. If a catastrophic disturbance does not occur, one may be able to document hydrologic succession or even cliseral phenomena, but primary or secondary succession, on a recognizable scale, would be missed. The profile for the Whiskey Creek section, documenting perhaps ten thousand years of forest history, is a case in point. Presumably massive disturbance in the Whiskey Creek area did not occur during the period represented by

the section exposed and studied. Although the pollen profile of the Whiskey Creek section, and the excellent macroflora preserved at several levels, provide an interesting record of hydrologic succession and climax vegetation dynamics, post-disturbance succession was not recognized.

Cliseral Model.—The final possibility to be discussed involves the consideration that, because of poor or insufficiently detailed temporal resolution, we are not looking at succession at all, but rather are dealing with long-term cliseral shifts in vegetation dominance. The data from the Type section indicate that the transition from mesic forest to vegetation of xeric aspect is not irreversible; the forest, in fact, returns eventually in that section. If the study sections represented time intervals on the order of millions of years they would then record pronounced climatic oscillations (mesic to xeric to mesic) on a scale never before suggested and the absence of a similar record from the Whiskey Creek section would be enigmatic. There is no evidence for evolution of Succor Creek taxa in the microfossil and macrofossil records, which is further evidence that a relatively short time is represented. Climatic oscillations in the short term, exceeding those of the Pleistocene, seem unlikely. The post-disturbance record is not a random sampling of xeric vegetation; rather, a directed sequence is discernible, consistent with known trends of secondary succession.

It might be argued that what is reflected are simply the equivalents of facies changes, indicative of depositional sites in an active fluvial or deltaic system with bars, levees, crevasse splays, or other features simply supporting different localized vegetation types. This might well be the case for a series of leaf floras, given the localized nature of leaf deposition, but this is unlikely when relative continuity of the pollen record is considered. During Whiskey Creek time, the sedimentary record indicates a high level of fluvial and lacustrine activity, yet no parallel phenomena of floral response to those local physiographic or edaphic changes can be noted, probably because the pollen record reflects the broader regional vegetation array. Succession, initiated by local volcanic activity seems to be the most uniformitarian and rational model for the data available.

Fire Initiated Succession

Although the major transitions in the Succor Creek pollen record have been attributed to volcanic disturbance over a wide area, fire as an initiator of localized succession is to be expected, particularly in areas supporting extensive conifer forests. In recent years increasing attention has been paid to the role of fire in regional vegetation dynamics (Bormann & Likens, 1979; Habeck & Mutch, 1973; Wright & Heinselman, 1973; Loope & Gruell, 1973; Swain, 1973; Rowe & Scotter, 1973). Fire is apparently a more frequent disturbance factor in coniferous forests and Rowe and Scotter (1973) note that fire incidence in mixed broad-leaved/coniferous stands increases with the proportion of evergreen trees in a stand. Daubenmire and Daubenmire (1968), referring to the forests of the northern Rocky Mountains, considered the probability of fire incidence to approach unity in a period of 450–500 years on a specific site. Hemstrom and Franklin (1982) reported a 465 year interval for natural fire rotation in the coniferous forests of Mt. Rainier (Washington). The most probable ignition source for such fires is lightning. Loope and Gruell (1973) stated that nowhere in the world is lightning a more significant

source of ignition than in the coniferous forests of the Pacific Northwest, citing rates of between 53 and 60% for lightning induced fires in this region. Rowe and Scotter (1973) noted that during one seven year period, 27% of all forest fires in Canada were lightning induced. Habeck and Mutch 1973, p. 410) stated that a high percentage of vegetation in all forest zones has been disrupted by fire and is at different stages of recovery. Forest stands that have reached climax or near-climax are only rarely found, and these only because those stands have fortuitously escaped fire for several centuries. He noted that past, uncontrolled fires did not usually create a completely burned over, denuded area at any one point in time as is evidenced by the many stages of development found in each forest zone.

Although fire may have been a disruptive influence on any of the forest types of the Miocene of the Succor Creek region, the Montane Conifer forests were probably most susceptible. Fire disturbance would most likely be reflected in a sudden decrease in Montane Conifer pollen levels, reflecting the loss of the source forest-cover type, followed by a recovery period. Loope and Gruell (1973) noted a pattern of initial pine dominance in burn areas in Wyoming, followed by a transition to spruce dominated forests with a gradual increase in the importance of fir. Such interactions might well be a factor in Miocene burns as well. In a well-watered area, disruption by fire would almost certainly be more limited than the widespread effects of ash falls and other secondary effects of volcanic activity and recovery might be reasonably rapid, with reseeding from surrounding areas not damaged by fire (Hemstrom & Franklin, 1982, p. 47).

One case that might represent a fire-initiated succession in the Succor Creek pollen record can be noted during the Montane Conifer/Bottomland Slope forest interval at the base of the Rockville section (Fig. 6). Here spruce pollen levels peak at over 50%, dropping to 10% in the next sample up the section (≈1.5 m). This sample also contains a large number of very small charcoal (fusian) fragments. Subsequent samples record a recovery in Montane Conifer pollen levels prior to the critical transition zone in the section. It is interesting to note that this abrupt Montane Conifer decline in the basal Rockville sediments occurs at a point where Pine starts a modest increase. This point is also marked by a small peak in Xeric pollen types. This very sharp oscillation in Montane Conifer levels might well represent a local burn, causing an abrupt decrease in the contribution of Montane Conifer taxa to the pollen record. Furthermore, the Xeric pollen peak may represent an influx of herbaceous plants into the burn area, followed by Pine and Montane Conifer elements. Over a period of several centuries one would expect Pine levels to drop as the Montane Conifer elements re-achieved ascendency and such a pattern is consistent with the pollen profile.

Although fire may play a role in defining the interaction of Montane Conifer and Bottomland/Slope elements, most of the oscillations between these two groups are more gradual in nature, suggesting the possibility of climatic control. This subject will be discussed in the following section.

CLISERAL SUCCESSION

Although the pattern of vegetation on a specific site may be modified by a variety of edaphic, biotic, or microclimatic factors, and by action of pseudo-

periodic agencies such as fire, wind, water and disease, it is a well-accepted concept in phytogeography that climate plays the dominant role in determining the nature of regional vegetation (Cain, 1944). Any significant change in the components of regional climate, mean and range of annual temperatures, annual precipitation, or shifts in rainfall distribution, can be expected to induce changes in the nature and distribution of vegetation in the region. The climatic control concept is so well-established that the nature of terrestrial vegetation as reflected in the fossil record serves as the primary means of reconstructing Late Cretaceous and Tertiary paleoclimates for continental deposits. Unfortunately even if the nature of a fossil flora is well understood, no linear conversions exist to transform a specific fossil data set into the context of world paleoclimate due to a variety of factors, including elevation, slope exposure, and the degree of thermal buffering provided by nearby seas or large inland lake systems. Tertiary paleobotanists have adopted two distinctly different approaches to resolve this dilemma and profound differences of opinion on Tertiary climatic trends have emerged.

The ecological school of paleoclimate, pioneered in the studies of Ralph W. Chaney and further refined by Axelrod (Axelrod, 1968; Axelrod & Bailey, 1969), postulates a period of gradual cooling through the Neogene with vegetation development modified regionally in the Pacific Northwest by the development of the rain shadow of the Cascades. In this model, cooling is accompanied by a decrease in equability and the only short-term changes in annual temperature that occur are the result of elevational changes related to uplift.

The foliar physiognomy approach to paleoclimatic reconstruction, led by Wolfe (Wolfe & Hopkins, 1967; Wolfe, 1978), postulates a sharp drop in mean annual temperatures in the Oligocene with relatively constant mean annual temperatures from that point to the present day. Wolfe (1978) suggested a pattern of mild late Tertiary mean annual temperature oscillations in his graphic presentation of the data (see also Dorf, 1959), but stated that altitudinal differences provided sufficient uncertainty in the Pacific Northwest record to preclude detailed conclusions. He did state however that the Miocene record is characterized by an increase in equability with drops in summer maxima counteracted by increases in winter minima.

We have stressed previously the evidence for a cool but equable climatic regime to reconcile the macrofossil and microfossil data for the Succor Creek Flora. While our data support the equability component of Wolfe's reconstruction (1978), we suggest somewhat cooler temperatures than he indicated for regional Miocene floras and the relative constancy of the thermal regime is open to some question. Definitive long-term thermal trends on the Succor Creek Flora have proved to be impossible to demonstrate with the data currently available. Shah (1968) and Smiley et al. (1975b) documented what they believed to represent a definitive cooling and drying trend throughout the middle to late Miocene based on a sequence of Miocene and Pliocene floras from the Weiser area of Idaho. The absence of Montane Conifer Paleoassociation pollen from the strata of the lower Type section record, and its presence in the upper part of the section led us (Taggart & Cross, 1980) to postulate a slight cooling trend through the time represented by the Sucker Creek Type section with early Type section temper-

atures being sufficiently high to exclude the Montane Conifer element from adjacent uplands. We noted that reduced elevation in the Type section area, coupled with modest topographic relief, might require only slightly higher temperatures to achieve such an exclusion. Although there is no reason to alter the assessment of the relative temperatures in early as opposed to late Type section time, new evidence from above and below the measured Type section makes it unlikely that this difference in temperature represents a definite trend.

Additional strata above the Type section have now been measured and sampled and an additional productive pollen sample located approximately 6.5 m above the top of the measured section has now been tabulated. This sample contains approximately 23.3% Montane Conifer, 55% Bottomland/Slope, 12.5% Swamp, 2.5% Pine, 2.5% Xeric, and 4.2% Other pollen. Therefore, this is comparable to the productive samples from the upper Type section already reported.

The top of the Rocky Ford section, a unit about 11 m thick, located across the Succor Creek Valley, correlates to within a few meters of the base of the measured Type section. Pollen spectra from two productive samples obtained from the unit are very similar to those from the Succor Creek sections to the south (averaging 39% Montane Conifer pollen) and indicate even cooler conditions than those in upper Type section time. Thus in the Type section area the pollen record indicates a cool interval during Rocky Ford time, followed by a warmer interval in early Type section time. By the time forest vegetation had returned following disturbance in middle Type section time, temperatures had dropped again, although late Type section time was apparently slightly warmer then during Rocky Ford time (Fig. 10). The pollen record from the Type section thus supports the same oscillatory temperature model discussed previously in terms of climax vegetation dynamics. It should be noted that although these thermal oscillations have very distinctive pollen signatures, the magnitude of the oscillations need not have been very great to have caused the observed pollen shifts if slope gradients were sufficiently low.

Marine studies of foraminifera and oxygen isotope ratios indicate definite thermal oscillations throughout the postglacial, the "Little Ice Age" being the most significant excursion of this sort in the historical record. Imbrie and Imbrie (1979) have suggested that such oscillations are the result of interactions of cycles in earth orbit mechanics (eccentricity, tilt, and precession) as proposed by Milankovitch (1930) as a theory to explain the origin of Pleistocene glaciations. Our studies indicate that considered in time, spans of thousands to tens of thousands of years, Miocene climates in the Pacific Northwest exhibited a similar oscillatory thermal regime. Given the magnitude of this oscillation and the limited time represented by the rocks of the Sucker Creek Formation, it is unlikely that the Succor Creek Flora, or any single flora for that matter, can provide definitive data on the existence of any overall trends superimposed on this pattern of thermal variability. Our data do suggest however that unless the scope of thermal variability for a fossil assemblage can be assessed, caution must be used in integrating the thermal indications of a flora into a regional model for climatic trends. This *caveat* would appear to be equally applicable to climatic modeling based on foliar physiognomy or ecological affinities.

GEOLOGIC CONSIDERATIONS

Physiography and Topography in Consideration of Regional Climate

The Columbia Plateau, Basin and Range, and Snake River Plain Provinces, which surround this Succor Creek area, are physiographic provinces established on the basis of some unifying fundamental geologic characteristics, as well as topographic features. The Succor Creek area is generally considered to be an eastward extension of the Columbia Plateau Province, but there is some evidence that it may actually be a part of the Basin and Range Province (see Fig. 3). The Owyhee Mountains seem to be isolated from the rest of the Plateau region as an island-like mass rising above the surrounding volcanic plateau.

Some attempts have been made to establish the paleoelevation of the Succor Creek region on the basis of the fossil flora. Axelrod (1964; 1966, text-fig. 12; and 1968, fig. 7B) considered the Succor Creek forests to have been developed at an elevation of less than 300 m, based on considerations of effective temperature and equability as indicated by the leaf flora. Axelrod (1966) defined the composition and altitudinal zonation of the dominant forest communities of the Miocene of the Columbia Plateau region as:

1. broad-leaved evergreen forests (below 150 m)
2. mixed deciduous hardwood forests (150–500 m)
3. montane conifer/deciduous hardwood forests (500–1,000 m)
4. montane conifer forests (above 1,000 m)

Our data indicate that the Succor Creek forests might be classified most appropriately as montane conifer/deciduous hardwood forest in the framework of Axelrod's 1966 terminology, probably near the high side of the 500–1,000 m zone. It is likely that the prevailing mean annual temperature and range of temperature was such as to permit the Succor Creek basins to support predominantly evergreen oak forests, with deciduous hardwood forests on adjacent low slopes, grading ecotonally into conifer forest of montane aspect on adjacent uplands of moderate elevation relative to the valley floors. Wolfe (1969, p. 93) argued that the Succor Creek Flora ("Rockville") was probably an upland area of at least "moderate elevation," based on geological considerations relating the Succor Creek deposits to those of the Latah, Mascall, and Fish Creek Floras. Their stratigraphic positions on or interbedded with the Columbia River Basalt indicate mid-Miocene elevations of 500–750 m. Wolfe and Hopkins (1967, p. 71) indicated that the percentage of entire-margined leaves in the Succor Creek ("Rockville") Flora is 30%, indicative of a temperate assemblage (Wolfe, 1969, p. 87). As we noted previously, there appears to be no valid reason for separation of the Succor Creek Flora into two or more temporally distinct assemblages. Taken as a whole, about 25% of the Succor Creek woody dicot leaf species have an entire margin, reinforcing the assignment of temperate aspect to the bottomland assemblage. Such an analysis, however, overlooks the variation in the composition of individual florules. Only a single Succor Creek florule, that from the Fenwick Ranch (Graham, 1965), has the requisite 30 dicot leaf taxa to justify quantitative analysis of leaf margin data within a 5% margin of error (Wolfe, 1971, p. 36). In that case, the percentage of entire margins in the dicot florule is approximately 30%. Only

two other florules have in excess of 20 woody dicot leaf taxa (McKenzie Ranch and the Carter Creek localities, Graham, 1965), and these show entire-margined dicot leaf percentages of 14% and 28%, respectively. This range of variability exceeds that used by Wolfe (1969) to demonstrate that the sequence of Neogene floras in the Columbia Plateau region represents variation in thermal regime with time, as opposed to the altidudinal zonation suggested by Axelrod (1964), and encompasses a range of climate from cool temperate to warm temperate (Wolfe & Hopkins, 1967).

We are not committed to either an altitudinal or temporal change model for any combination of the Neogene floras of the region, but we consider that the data available are simply too variable to suggest unambiguous validation of either model. Both pollen and leaf-margin data suggest that the climax vegetation, supported on any specific site within the Succor Creek area, was variable, and subject to a variety of site factors. We know, on the basis of the stratigraphic studies of specific sections, that the development of specific forest types was subject to modification based on short-term climatic fluctuations and the action of disruptive events such as volcanic disturbance and fire. To the extent that similar variability can be assumed to exist in other areas within the region throughout the Neogene, generalizations simply are not justified where they are based on small numbers of pollen spectra, on isolated, individual floras, or particularly, where based on "composite" assemblages where routine taxonomic treatment tends to mask florule diversity. Such generalizations may be misleading in the context of a single flora, suggesting the need for caution in the creation of broad regional models of any sort.

We have postulated the area to have been a low-gradient upland plateau during mid-Miocene, possibly a northward or northwestward sloping paleoslope (Taggart & Cross, 1980). This upland must have had either a high enough elevation or a climate cool enough to support, at least intermittently, a montane conifer forest within a few km of the fluvial and lacustrine sedimentary basins in which the macrofossil floras accumulated. To account for this, we will evaluate some other geological features of the area that suggest a greater elevation of the region during Succor Creek time.

Principal Structural Features Relevant to Succor Creek Vegetation Development

The tectonic history of the Succor Creek area is intimately related to the Basin and Range Province to the south and west, to the Snake River Plain to the east, and to the Columbia Basalt Plateau to the north (Fig. 3). A major tectonic boundary in this area marks the western margin of the continental craton and the eastern edge of the Phanerozoic "eugeosyncline." This line has been identified as extending in a general north–south direction and passes just east of the Oregon-Idaho state line. This suture, or margin of two adjoining crustal plates, passes directly through the Owyhee Mountains (Fig. 2) and the eastern portion of the Succor Creek area (Armstrong et al., 1977, fig. 10; Davis, 1979, fig. 2). This line also crosses the Snake River Plain near its western end and may possibly be related to some structural features of that graben. Armstrong et al. (1977) and

Davis (1977, p. 4) have postulated the position of these plate margins within 10 km on the basis of the ratios of Sr^{87}/Sr^{86} in igneous rocks of the area. Later rocks are mostly of Mesozoic age in the southeastern Oregon-southwestern Idaho area. Ben-Avraham (1981) proposed that an exotic sliver or fragment (microcontinental plate) of allochthonous terrain adjoins the Precambrian North American plate on the west at this suture. Davis further suggested (1977, p. 35) that this suture is a zone of crustal weakness that was reactivated in Miocene times during the ENE–WSW regional extension. Davis (1979, p. 43) also noted that the dike swarms in eastern Oregon-western Idaho, from which most of the eastern area of the Columbia River Basalts were probably extruded, lie directly west of this north–south tectonic boundary. The southern margin of the dike-swarm area lies about 25 km north of the Succor Creek area. On the basis of gravity and magnetic anomalies, Mabey (1976, p. 55) postulated a thick layer of basaltic rocks of probable Miocene age, directly north of the Succor Creek area, possibly a remnant of a more extensive sequence, preserved by subsidence of the western end of Snake River Plain, probably with basaltic accumulation concurrent with subsidence. The outpouring of the basalt probably accompanied rifting of the upper crust under the Plain, which resulted from NE lateral spreading. If this is correct, the western Snake River Plain was a rift in Miocene time. In the northern part of the Succor Creek area, this subsidence may have been accompanied by penecontemporaneous accumulation of silicic ash deposits and weathered residuum by fluvial transport from the Idaho Batholith (Kittleman et al., 1965).

This tectonic boundary or suture is a zone of weakness through the crust, whether or not it was reactivated in mid-Miocene time. It could be the locus for the origin of a mantle plume from the asthenosphere or a propagating fracture system. Mantle plumes may be part of the non-arc related zones of continental rifting, or transform faults such as the Snake River Plain (Fig. 13). Morgan (1972) estimated the mantle plume, now located under Yellowstone National Park, to be about 150 km diameter, and to be rising at the rate of about 2 m/yr from deep in the asthenosphere into the lowest part of the mantle. More pertinent is Morgan's proposal that the Yellowstone mantle plume is structurally related to the northeast end of the Snake River depression. He considered that it arrived at this position after traversing southern Idaho along the course of the Snake River Plain. He and others (Suppe et al., 1975) considered the North American plate to have moved generally westward across a mantle plume that originated in the Owyhee area, at the position of the above mentioned suture, about 15 to 20 million years ago. The rate of eastward net migration of the mantle plume under the Snake River Plain was estimated at about 2.5 cm/yr by Armstrong et al. (1975).

Kirkham (1927, 1931) first postulated the Snake River Plain to be a downwarped plain, depressed to about 6,000 m below sea level. However, later studies clearly demonstrate the extensive, *en echelon*, NW-directed faulting, and any downwarp probably developed immediately prior to or concurrently with the deposition of the Sucker Creek Formation. This would account for the very rapid northward thickening of the Sucker Creek surface-type volcaniclastic sediments deposited in the western end of the depression.

Suppe et al. (1975) noted that the lowest stratigraphic unit in this region of Idaho is clearly associated with this propagating fracture or migrating hot-spot

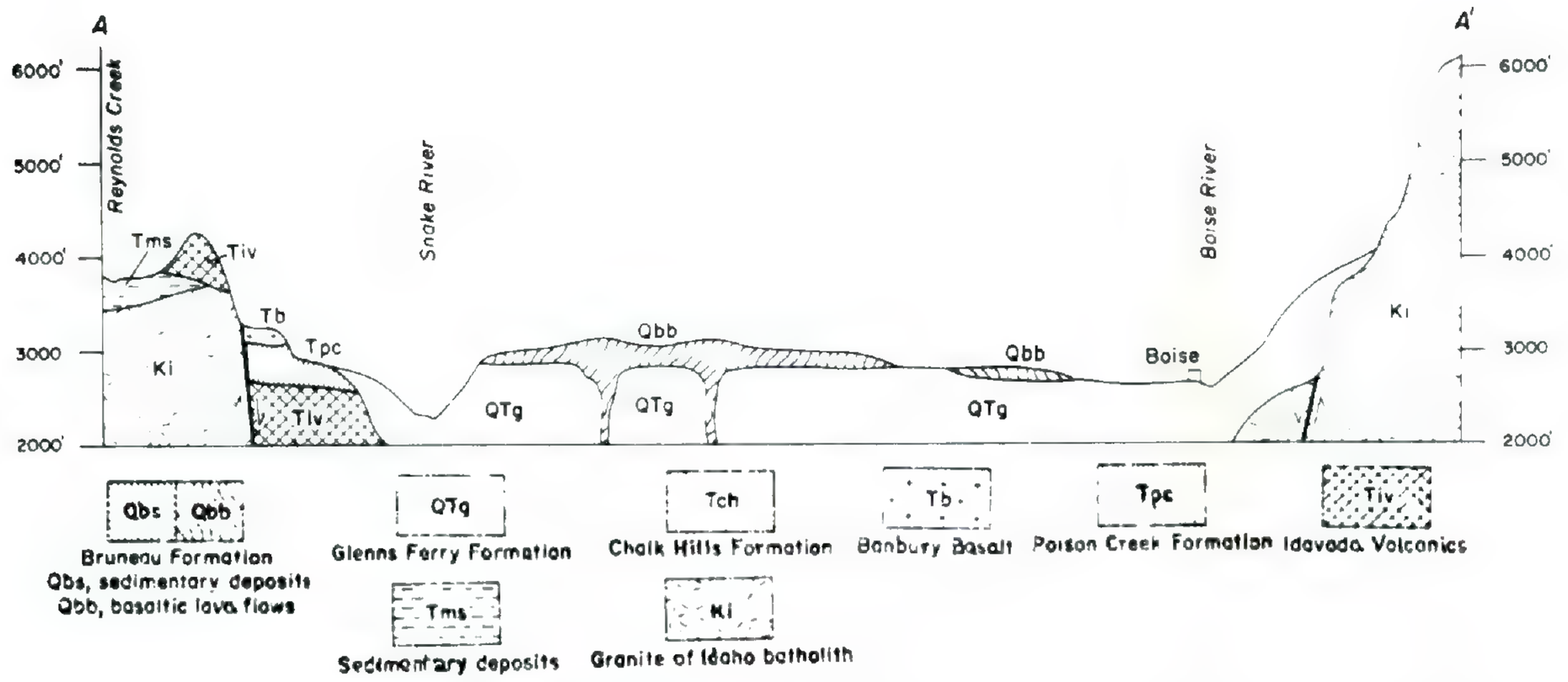


FIGURE 13. Diagrammatic geological cross-section from Reynolds Creek across the Snake River Plain through Boise, Idaho, showing the relationship of the graben structure of the Snake River Plain to the surrounding "horst" blocks. The Tms pattern at the far left represents the Sucker Creek Formation and possibly later sedimentary formations (Pliocene Poison Creek Formation). The Pliocene Idavada Volcanics (Tiv) overlie the Miocene sedimentary rocks unconformably. The basement rocks here are Cretaceous and earlier granites of the Idaho Batholith. Welded-ash flows of the Idavada Volcanics locally overlie the Sucker Creek Formation northwest of the Owyhee Mountains in a similar fashion as indicated on the cross-section just east of Reynolds Creek. (From Malde & Powers, 1962, Upper Cenozoic strata of the Snake River Plain, Idaho. Bull. Geol. Soc. Amer. 73: 1203, fig. 2.)

and is the earliest deposited portion of the time-transgressive Idavada Volcanics that overlie the Sucker Creek Formation in the western Idaho region. The age has been determined as early Pliocene on the basis of vertebrate fossils (Malde & Powers, 1962). These volcaniclastics are restricted to the uplands north and south of the Snake River and are cut by northwest trending faults that are probably related to the diastrophism that outlined the western Snake River Plain (see Fig. 3).

Suppe et al. (1975), following Morgan (1972), have reasoned that the Snake River Plain downwarp developed in the wake of the northeastward moving mantle plume at 2.3–2.7 cm/yr toward the Yellowstone area where it is today. They suggested the migrating domal uplift associated with the hot-spot is about 150–300 km in diameter, and the elevation of the updome above the region to the north and east of Yellowstone today is about 2 km maximum.

If this analogue is applied to the Oregon-Idaho border area at the time of the initiation of the dome, 15 to 20 m.y.b.p., the Owyhee and Succor Creek area may have had similar ephemeral elevation in mid-Miocene, which decayed in 3–4 m.y. to more nearly the present elevation, as the North American plate moved northwestward above the plume. If the domal uplift was initiated at the suture line of the Precambrian-Phanerozoic boundary in the vicinity of the Owyhees, there also may have been a westward or northwestward tilt of plateau-like proportions of this whole region, a paleoslope dipping off this ephemeral dome in a manner similar to that postulated for the Colorado Plateau by Suppe et al. (1975, p. 424).

A second basic explanation for the development of the Snake River Plain–Yellowstone system was proposed by Smith (1977) and Christiansen and McKee (1978). The essence of this concept, which also may result in conspicous elevation

of the caldera, is that the system is a plate interaction phenomenon (Christiansen & McKee, 1978, p. 306). This interaction of the North American, Pacific and Farallon (Juan de Fuca remnant) plates began at least 29 m.y.b.p., but from about 17 m.y.b.p. the principal stress has been between the North American and Pacific plates. This resulted in two zones of lithospheric extension and stress relief at the northern margin of the Great Basin, a transform boundary; the Snake River plain to the east, and the Newberry system to the west, which is essentially coordinate with or parallel to the Brothers Fault zone (Fig. 3).

Iyer et al. (1981) have identified the presence of a large, low-velocity, magmatic body under the Yellowstone caldera, which may extend only to a depth of 200 to 300 km. The top of this partially molten body has been estimated at about 10 km. One possible model involves a region (or regions) of melting in the asthenosphere, upward migration of the magma, and secondary large-scale melting of the lower crust. Though this model and these interpretations would rule out the Morgan (1972) and later postulations of a deep mantle plume (hot-spot) or chemical plume (Anderson, 1975), and other explanations, it would support the proposals by Green (1971), Smith (1977), and Christiansen and McKee (1978), that the Snake River Plain–Yellowstone caldera are part of a propagation fracture system of the lithosphere, through a series of northeastward migrating calderas, with Yellowstone at present at the northeastward end of this fracture. This system is presumed to have followed a pre-existing zone of weakness (transform fault?) in the lithosphere.

This model does not require significant upwelling but does invoke thermal expansion under or near the zone of stress. But the development of calderas at successive stations along the route of propagation (here along the transform boundaries) is usually accompanied by ephemeral uplift and eventual collapse. Pelton and Smith (1979) in a review of possible causes of uplift associated with hot magmatic bodies underlying calderas, noted that the present Yellowstone caldera is 80–100 km maximum diameter, but other Snake River Plain caldera are estimated at 150 to 300 km. They also document the uplift of the Yellowstone caldera at the average rate of 14 mm/yr since 1923 (=1,400 m/100,000 yr). This time frame and magnitude of uplift greatly exceed that which would be required for distinctive shifts from bottomland/slope deciduous and evergreen dicot floras to montane conifer-dominated vegetation, postulated for the Succor Creek region in mid-Miocene.

Paleoelevation Variation of the Succor Creek Depositional Sites

We have postulated cool but highly equable climatic conditions for the Succor Creek region during the middle Miocene. Additional uplift in the Succor Creek area, relative to the present elevation of the region, would be required to obtain the cool thermal regime implied by the flora. Normal thermal lapse rates are of the order of 0.65°C/100 m (Miller & Thompson, 1975), and we suggest the character of the pollen flora indicates the Miocene elevation of the region must have been in the range of several hundred to 1,000 m higher than today.

Disparity between presumed paleoelevation of Miocene and Pliocene floras and present elevation of a region are not uncommon. A relatively low elevation

Miocene surface (i.e., below 600 m) was identified by Axelrod (1962) on the basis of fossil vegetation data for the Lake Tahoe area of California, which presently has an elevational range of 1,500 to 3,000 m.

Geological evidence provides several possible factors, some of which may be interrelated, that may have resulted in a distinct elevational differential between the Succor Creek region and surrounding areas. One factor may have been the development of a basin area to the north of the Succor Creek region due to the northwestward extension of the Snake River Plain rift or graben structure. There is ample evidence that sufficient downwarp or graben-type basin developed concurrently in the mid-Miocene to accommodate accumulation of 1,500 to 2,000 m of volcaniclastic rocks in the Sucker Creek Formation (Warner, 1977). The relative thinning of the formation southward in the Succor Creek area indicates a difference in elevation of several hundred meters. The Succor Creek area may have been subjected to significant uplift contemporaneous with the development of the flora. Brott et al. (1978, p. 1706) postulated that, beginning about 18 m.y.b.p., the Oregon-Idaho border area rhyolitic ash-flows must have been associated with ". . . a regional uplift of several hundred meters above the surrounding terrain, caldera formation at the source of the extrusives, and large-scale hydrothermal activity . . . ." This center of rhyolitic volcanism moved gradually eastward and, after 3–4 m.y., the area surrounding the original scene of eruption had subsided by 500 m or more.

Paleobotanical evidence for cool but equable climates appears sufficient to support this interpretation for the Succor Creek Flora. This is discordant with the somewhat warmer, but similarly equable, paleoclimates postulated for other contemporaneous floras in the region. However, sufficient structural evidence exists to provide a rational explanation of this anomaly. The elevation of an area need not remain constant, even over relatively short time spans, and such factors must be considered in analysis of Tertiary climates based on geographically and temporally distinct floras.

Volcanic Episodes as Related to the Succor Creek Flora

Mid-Miocene volcanism was an important event throughout Oregon and Washington, and, in theory, over a great part of the circum-Pacific area (McBirney et al., 1974, p. 587). The most intense volcanic episode in the Miocene is coincident with and directly related to the Columbia River Basalt outpourings, dated by Watkins and Baksi (1974) as beginning about 16.7 m.y.b.p. and lasting about 2.5 m.y. A corresponding and related center of activity to the Columbia River Basalt episode was located further west in the Western Cascade Mountains. There, a thick sequence of andesitic lava, the Sardine formation, comprises the main body of volcanic rocks in that region. These two great sequences of volcanic extrusives represent the most intense volcanism of the Pacific Northwest in Cenozoic time (McBirney et al., 1974, p. 586). The silicic lavas, ash-flows, and tuffs of the Succor Creek area and surrounding regions, south of the Columbia River Basalts (Fig. 3), represent episodic outbursts over much of this same time period. The source of these volcanics has been extensively occluded by accumulations during two much more recent extended episodes of volcanism, late Miocene–

Pliocene (9–11 m.y.b.p.) and late Pliocene–Quaternary (3.4–5.7 m.y.b.p.). The positions of some of the latter andesitic cones are indicated between the siliceous tuff fields on Figure 3.

Davis (1977, 1979) noted that, on the average, the Columbia River Basalt flows may have erupted every 10 to 20 thousand years with an average outpouring of 10 to 20 km^3. Some single flows were even larger, at least one reaching the Pacific ocean near the mouth of the Columbia River (Davis, 1977, p. 33; 1979, p. 43). The magnitude of this episodic destruction and the widespread distribution of even single flows, which repeatedly destroyed the vegetation over several thousand km^2, is difficult to comprehend. It is also possible that the siliceous tuffs, ash and rhyolites, which erupted south of the main expanse of the Columbia River Basalt field (Fig. 3), throughout the area of the Sucker Creek Formation, had a similar episodic time frame. We have estimated an 8,000 and 10,000 year period of accumulation of the 200 m thick Sucker Creek Type section and 100 m thick Whiskey Creek section, respectively. There may be more than coincidence in the similarity of episodic time intervals postulated, for the deposition of the plant-bearing ash and tuff beds, which have been derived from two different lines of evidence. Episodic volcanism is well-represented in the Succor Creek area. At least 16 successive lava flows of middle Miocene age make up the Owyhee Basalt near the Owyhee Reservoir, just west of the Type section (Watkins and Baksi, 1974). The earliest lava (no. 16) has Reverse paleomagnetic polarity; lavas no. 15 up through no. 3 have Normal polarity; the two uppermost are transitional. The time interval represented by the 16 flows and the intervening unconformities, is not more than 0.8 m.y. (13.9–13.1 m.y.b.p., Watkins & Baksi, 1974).

In both the Columbia River Basalts and the siliceous pyroclastic deposits of this area, it is probable that only small portions of the total area of distribution of the Sucker Creek Formation were buried by tephra from each eruption, but in successive eruptions alternate areas were covered. The extent of peripheral destruction of vegetation around the perimeter of each successive area buried under the pyroclastics was probably much more widespread than that from the recent Mt. St. Helens episode.

There is good evidence that geological factors, i.e., direct or side effects of tectonics and volcanism, may have contributed to the cooler episodes indicated by the presence of the Montane Conifer Paleoassociation in the Succor Creek Flora. It is possible that the cooling of the regional climate is directly attributable to sustained clusters of volcanic episodes that were the source of injection into the upper atmosphere of enormous quantities of very finely divided ash particles (discussed in the following section on Sedimentation). Robock (1979) demonstrated good correlation of the amount of volcanic dust in the atmosphere with average surface temperatures of the Northern Hemisphere during the past 400 years.

Flohn (1979) proposed that the intensified stratospheric dust layers resulting from volcanic eruptions may cause very rapid changes of temperature, with the intensity of cooling reaching the order of 5°C/50 yr, and a duration of centuries for such cool periods. The cooling results from both absorption and backscattering of part of the sun's radiation by the "dust veil" (Flohn, 1979, p. 140). He suggested that the frequency of such episodes may be on the order of one- to ten-thousand years. Though his study was directed toward explanation of sudden

cooling in interglacial periods over the last 7×10^5 yr, he suggested that very rapid cooling and maintenance of cooler climate for such periods is not restricted to the Pleistocene. Such events may be related to periods when "clusters of volcanic eruptions" have occurred. Axelrod (1981) indicated it is unlikely that single volcanic events have had more than ephemeral climatic effects.

Bray (1979) discussed another factor influencing the lowering of temperatures as a result of volcanic activity, which is considered here in respect to its possible effect on vegetation destabilization. He suggested the increase in albedo, which would have characterized the regions covered by extensive, light-colored, ash deposits from eight particular eruptions during the Pleistocene, would have ranged from about 0.06% to 0.41%, depending on the reflectance quality of each different ash blanket. Such increases in albedo would have lowered the temperatures regionally from 0.07° to 0.41°C, with greatest cooling in and surrounding the ash-covered terrains. The extent of ash coverage for each volcanic event may vary considerably and the accompanying albedo-induced lower temperatures persisted for many decades (Bray, 1979). The rhyolitic ash layers of the mid-Miocene are believed to have been very widespread in eastern Oregon–western Idaho (see Fig. 3), and were very light-colored.

Regional increases in surface albedo, coupled with world-wide increases in atmospheric albedo can be assumed to be cumulative in their local effect. Where sufficient elevation was present, such as the ephemeral uplift of the region discussed previously, still further temperature depressions coincident with and following volcanic episodes might be expected. Regional snowfall may well have increased, leading to more extensive and persistent snowfields, which would have further increased regional surface albedo, intensifying the cooling produced by the surface ash layers. All of these phenomena are consistent with the expansion of the areal extent of the Montane Conifer Paleoassociation at different periods during Sucker Creek time.

Axelrod (1981) made extensive analyses of the historic effects of volcanism and its effect on terrestrial and marine life, particularly due to lowered temperatures as a result of episodes of extensive volcanic activity. He stressed the importance of the location of the volcanoes ("circulation tends to restrict dust veils resulting from Northern Hemisphere middle- and high-latitude eruptions to the regions north of lat 30°N, whereas dust from low-latitude eruptions . . . spreads over the entire globe . . . ," 1981, p. 1); the height of injection of the tephra into the atmosphere; and the size of the particulates of the ejecta. He noted that in addition to the cooling effect of decreased radiation reaching the earth's surface, the infrared energy radiated back from the surface is not contained by the atmospheric dust blanket.

Axelrod (1981) summarized the mid-Miocene changes in vegetation in the far Western Interior, including the Pacific Northwest, noting that thousands of km^3 of volcanic ash in the upper atmosphere lowered the mean temperature, which brought colder winters. This also strengthened the sub-tropical high-pressure cell, so that the frequency and amount of warm-season convectional precipitation also decreased. This would accelerate the disappearance of many of the warm-temperate to subtropical deciduous evergreens from the flora and result in a broad expansion of montane conifers at higher altitudes. We have noted the continued

FIGURE 14. Lacustrine sediments in the Succor Creek area. Most lacustrine units in the study area are recognized on the basis of the generally thin-laminated, fine-grained sediments making up the strata, but outcrop exposures are typically too limited to indicate the geographic extent of the lake system. This shows a major outcrop of lacustrine sediments exposed in the Coal Mine Basin about 3 km east of the Whiskey Creek section (Fig. 1). The sedimentary laminations of this deposit are visible on the foreslope in the lower left of the picture. This unit consists of approximately 45 m of sediment and was sampled at intervals averaging approximately 50 cm. Some of the pits excavated to recover a continuous sequence of samples are visible on the slope face on the left side of the photograph. A total of 13 leaf-bearing horizons were documented within this unit.

presence of all these floristic elements in the region through Sucker Creek time, with repeated oscillation of the Montane Conifer Paleoassociation with the Bottomland/Slope community.

Sedimentation and Alteration of Sucker Creek Rocks

The source of the sediments that comprise the Sucker Creek Formation and the presence of fossils in some layers and their absence in others require some explanation. The Type section is adequate as a basis for discussion of most of the sections we have studied (Fig. 1). Kittleman et al. (1965) described in detail the lithologic, petrographic, and some mineralogic characteristics of about 25 of the definable beds in this section. We have restudied the exposures in the area, filled in some lithologic information of the concealed zones of Kittleman et al. from traceable beds in related exposures, and extended the base and the top of the section to include additional strata above and below. We simultaneously collected about 70 samples from the various layers for palynologic analysis. Some samples represent subdivisions of certain lithologic units defined by Kittleman et al., as indicated in Figure 10.

Most of the strata in this section are comprised of fluvially transported ash and pumice and some lacustrine deposits. A few beds were deposited directly

FIGURE 15. This shows a closer view of evenly-laminated, porcelaneous, lacustrine beds near the junction of Rte. 95 and Succor Creek road (Fig. 1), an early site for collection of Succor Creek plant macrofossils. Some of the layers within this sequence are indurated with chert, and typical Succor Creek leaf material occurs throughout. Pollen samples from this interval record a suite dominated by Bottomland/Slope and Montane Conifer elements, typical of the "climax" forest pollen signature throughout the area.

from air falls. Some of the layers are comprised of the finer size sediments, such as ash or pumice, flushed off the topographic highs and fluvially transported into the valleys and lower basins. Weathered materials from basaltic and rhyolitic flows and injections, and from extensive welded-ash beds from nearby areas, also contribute to some of the strata here.

A number of these beds contain fossil spores, pollen, fragments or burned shards of woody tissues of higher plants (fusain), and some algal cells and cysts including dispersed diatoms and massive layers of diatomite. A few beds contain larger fossils of fish, mammals and disarticulated vertebrates, and plant leaves, seeds, fruits, twigs, larger slabs of wood, and stumps. The larger plant remains usually occur in lignites, lignitic shales, lake beds (comprised of volcanic claystones (Figs. 14, 15), mudstones, siltstones, and diatomites), and occasional fluvial deposits. However, many of the lithologic units, comprising a significant portion of the thickness of the 200 m of exposed volcaniclastic rocks in the Type section, are barren of organic detritus. Pollen, spores, and woody detritus (fusain and vitrain) may have originally been present in many of these strata, which are now barren, though probably in very low percentages, volumetrically, due to a major dilution factor in beds of rapid ash accumulation. Entrapment of larger plant fragments may have taken place where the air-fall or water-laid ash accumulated over forest floor litter or where vegetation was killed and stripped by vented gases or hot or gaseous ashflows and was blown or washed into lake or fluvial basins.

Petrographic evaluation of various beds indicates a possible explanation for

the absence of fossils from large portions of this 200 m section and other areas. The layers of pyroclastic sediments have been altered to variable extents. The ejected pyroclastics are comprised of fresh glass shards, formed from stretched and exploded glass bubbles, and angular pumice in a mixture of size fractions and mineral composition. Some of the beds in the Type section are largely comprised of such pumice (units K-20, K-29, and K-31, Figure 10, are predominantly unaltered glass shards in silvery-gray pumice). These contain no fossils. Many of the beds are extensively altered, mineralogically, often to 70% to 90% clay materials of several types. Bed K-14, for example, has 80% clay with some subhedral plagioclase, some coarse-grained, clear, angular quartz, and abundant authigenic zeolite minerals such as clinoptilolite, and some clasts of mafic or silicic scoria and rhyolite (Kittleman et al., 1965). Bed K-9 is very similar mineralogically, but slightly less altered and with definable relic glass texture. This layer contains no plant fossils but a considerable number of water-distributed, disarticulated (some waterworn) vertebrate bones. Bed K-11 is an altered pumiceous lapillistone which probably originated as an air fall.

The presence of zeolite minerals, devitrified pseudomorphs of glass, high clay content, and occasional plagioclase feldspar (andesine) such as in beds K-9, K-13 and K-14 (Kittleman et al., 1965), gives a strong indication of very rapid alteration of the minerals in some zones. Hay (1963, 1978) has assigned most natural zeolite mineral occurrences to one of six types of geologic environments or hydrologic systems, three of which may be represented in the Sucker Creek stratigraphic sequence: saline-alkaline lakes; saline-alkaline soils; and percolating water in an open hydrologic system (such as the John Day Formation strata, which are similar to and 120 km northwest of Succor Creek). The zeolites form rapidly during and after burial or accumulation and in saline-alkaline lake environments, through the action of dissolved sodium carbonate-bicarbonate in a pH of about 9.5. Vitric tuffs may alter to zeolite under such conditions in less than a thousand years (Hay, 1978, p. 137). Surdham and Sheppard (1978, p. 152) noted that along Pleistocene Lake Tecopa, California, fresh glass occurs along the margin and inlets of the ancient lake. Thus, these different phases of alteration may be virtually penecontemporaneous, geologically speaking. Mumpton (1978) noted that Sheppard and Gude (1968) have correlated zeolite mineralogy with similar patterns in a number of western states of the United States.

Such rapid and extensive alteration in any sediment will be detrimental to many types of fossil remains. Pollen and spores are particularly degraded in high pH environments. Some of the water-laid volcanic ash beds, constituting a significant part of the stratigraphic sections that we have studied, are so extensively altered that it is not surprising they are barren. The post-depositional geochemical environment is therefore incompatible with the preservation of pollen and spores in many of the fluvial and lacustrine volcaniclastic rocks in this region.

MODERN REGIONAL ANALOGUE OF SUCCOR CREEK COMMUNITIES

The proposed post-disturbance successional hypothesis requires spatial and temporal intermingling of broad-leaved, coniferous, and xeric community elements on a topographically variable landscape. Although the assumed paleoclimax communities are typically of higher floristic diversity than extant commu-

nities, the Succor Creek area does support communities that are analogous in aspect to some components of our Miocene vegetation reconstruction. The extant vegetation of the Succor Creek region, below 1,500–1,800 m is a sagebrush-grass-forb steppe. A juniper-sage savanna vegetation is present erratically above about 1,600 m elevation, depending on the degree of protection by slope exposure and the size of the area. Woodland-shrub riverine communities appear beginning at slightly lower elevations. The present regional sagebrush-grass-forb vegetation is quite unlike the diverse vegetation array characteristic of Miocene climax communities constituting the Succor Creek Flora but is probably similar in aspect to the early post-disturbance sere. Other analogues may be noted in the Silver City area of the Owyhee Mountains in Idaho, south of the Succor Creek silicic volcanics (Fig. 3). Elevation throughout most of the Succor Creek region is about 1,200 m, but granitic peaks in the Owyhee Range rise to over 2,400 m. The Snake River, 30–35 km north northeast of the 2,450 m War Eagle Peak near Silver City, Idaho, is at 685 m elevation, and the broader reaches of the lava-covered Snake River Plain here (see Fig. 13) are between 750 and 850 m. Therefore, in 25 km, the topographic relief above the Snake River Plain is over 1,600 m.

The western side of the range supports increasingly diverse woody vegetation above 1,500 m due to the generally lower temperature regime and reduced evapotranspiration in the uplands. Figure 17 shows one site, at an elevation of 1,625 m, that supports a variety of community types somewhat analagous in aspect to the vegetation postulated for the recovery periods following disturbance in Succor Creek time. Dry, south-facing slopes (Fig. 16) support the sagebrush-grass-forb steppe characteristic of the region, with *Juniperus* widely scattered on the slopes. The limited riparian zone along the course of Jordan Creek supports a surprisingly diverse broad-leaved element including *Salix* (several species), *Populus* (2 species), *Acer*, *Alnus*, *Mahonia*, *Prunus*, *Ribes*, *Rosa*, *Rubus*, and *Sambucus*. The overall aspect of this riparian assemblage may be similar to that of the post-disturbance vegetation of the Miocene, except for the much greater diversity of the Miocene assemblage. Somewhat more mesic north-facing slopes (Fig. 17) support forests of *Pseudotsuga*, with an admixture of *Picea* and *Abies* above 1,800 m. The present montane forest is undoubtedly similar in aspect to that of the Miocene although *Pseudotsuga* has not been recognized in the fossil flora to date, and *Pinus* is missing today from the Owyhee area. The absence of pine from the extant flora appears to be a result of having been eliminated by the raising of the dry-line below, a condition that probably developed during the hypsithermal period (Bowman, 1911, pp. 206–207; Daubenmire, 1978, p. 172). The effect of this high "dry-line" below and a static or low "cold-line" above was to "squeeze out" the pine. Pine apparently has been unable to recover across the xeric barrier of the sagebrush-grass-forb steppe.

Conclusions

Historically, the individual macrofossil florules from the Succor Creek area have generally been treated as a single entity, the Succor Creek Flora. Such a single grouping of the florules is justified, based on the limited geographic distribution of the florules and the relatively limited time span (1–2 m.y.) represented by episodic volcaniclastics and flows totalling between 600 and 1,800 m in thick-

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FIGURES 16–17. Modern vegetation in the Owyhee Mountains east of the Succor Creek area. Both of these photographs, taken along the course of Jordan Creek at approximately 1,700 m elevation, show a mosaic of community types with floristic composition remarkably like that of some of the Miocene communities, when allowances are made for the absence of "exotic" taxa in the extant communities. The drier south-facing slopes shown on the left of Figure 16 support a sagebrush-

ness. With due recognition of spatial, elevational, and temporal variation between florules, the collective flora does represent a meaningful data set. Treating the complex in this manner, however, obscures a great deal of additional data that is critical in any interpretation of the flora relative to paleoclimatic trends or the pattern of modernization of floras within the region. The record of paleoclimatic trends during the one to two million year span of Sucker Creek time is now represented by discontinuous series of deposits, each laid down in a few thousand to a few tens of thousands of years.

Episodic volcanic disturbance and, to a lesser extent, other disturbance factors such as fire and localized flooding, resulted in periodic destabilization of forest habitats, with the consequent widespread occurrence of distinctive successional communities. Volcanic ash input, by air-fall or fluvial transport to local sedimentary basins and lakes, preserved plant macrofossils that represent some of the component species of localized communities that were part of the "climax" mosaic, as well as communities of a successional nature. Much of the recorded diversity of Succor Creek macrofossil florules can be attributed to disparate sampling of community types, together with disproportionate distribution and preservation of plant parts.

Unfortunately, the Succor Creek Flora, and most of the classic middle and late Tertiary floras of the Pacific Northwest, have lacked the close stratigraphic and palynological control required to recognize the presence of such community disruptions and the consequent successional vegetation dynamics. The fact that the floras in the region are preserved in fluvial volcanic ash deposits and volcaniclastic lake sediments, sometimes interbedded with diatomaceous beds strongly suggests that such disruptions and processes can be expected to have been widespread in occurrence. Many floras do represent samples of climax communities. However, if significant variation in diversity and composition exists between various florules of a flora, due consideration should be given to the possibility of the existence of distinctive communities representing seral stages. Only when climax associations can be identified with reasonable certainty, can meaningful regional paleoclimatic reconstructions be made. Postulating climatic trends based on stratigraphically disjunct and/or geographically distant floras of unknown relationships, as has been the practice, results in extensive obfuscation of the true nature of both short and long-term shifts in plant communities. Our studies indicate that in the short-term, centuries to tens of thousands of years (or even on a scale one order of magnitude greater), small-scale oscillations in temperature parameters characterized the climate of the Pacific Northwest during this part of the Miocene. Although the causes of such small-scale temperature oscillations are conjectural, it is reasonable to assume that temperatures in the region were controlled by some of the same factors operating today; i.e., elevation, relief, continentality,

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forb community with scattered *Juniperus*. The stream valley, lower right of Figure 16 and foreground of Figure 17 supports a reasonably diverse array of broad-leaved woody taxa including *Salix*, *Populus*, *Alnus*, and *Ribes*. North-facing slopes (upper right of Fig. 16 and Fig. 17) support stands of *Pseudotsuga* with scattered *Picea* above 1,800 m.

shifts in albedo caused by extensive new ash deposits, reduced insolation following volcanic eruptions, and earth orbit mechanics.

In areas of great topographic relief, such small-scale thermal changes would have a minimum effect on total vegetation components of a region. Where slope gradients are high, modest changes in the elevation of ecotones need not result in significant changes in the areal extent of specific communities and most communities could continue to find suitable niches in the variety of microenvironments in the valleys and protected slopes of a mountainous terrain for their general continuance. In contrast, where broad, sloping plateaus, or perhaps highland areas with very low relief, which we have postulated here, or in other places where areally extensive low-slope gradients characterize a region, even small regional temperature changes can cause pronounced areal shifts in community distribution. This would be particularly true for the various communities making up the regional vegetation mosaic, many of the components of which were under thermal stress near the margins of critical thermal fields.

The Succor Creek flora was, like any extant flora, a diverse mosaic of community types in dynamic equilibrium with climate. However, the vegetation was subjected to episodic and probably massive physical disturbance, which served to mold the dynamics and composition of the flora independent of cliseral shifts in community distribution. This situation was undoubtedly not confined to the Succor Creek area but was probably a regional phenomenon. Consideration of this dynamic response to disturbance, in concert with factors such as geographic, elevational, and temporal differences between Tertiary floras in the Pacific Northwest, may materially assist in the problem of modeling Tertiary climatic trends and vegetation modernization within the region.

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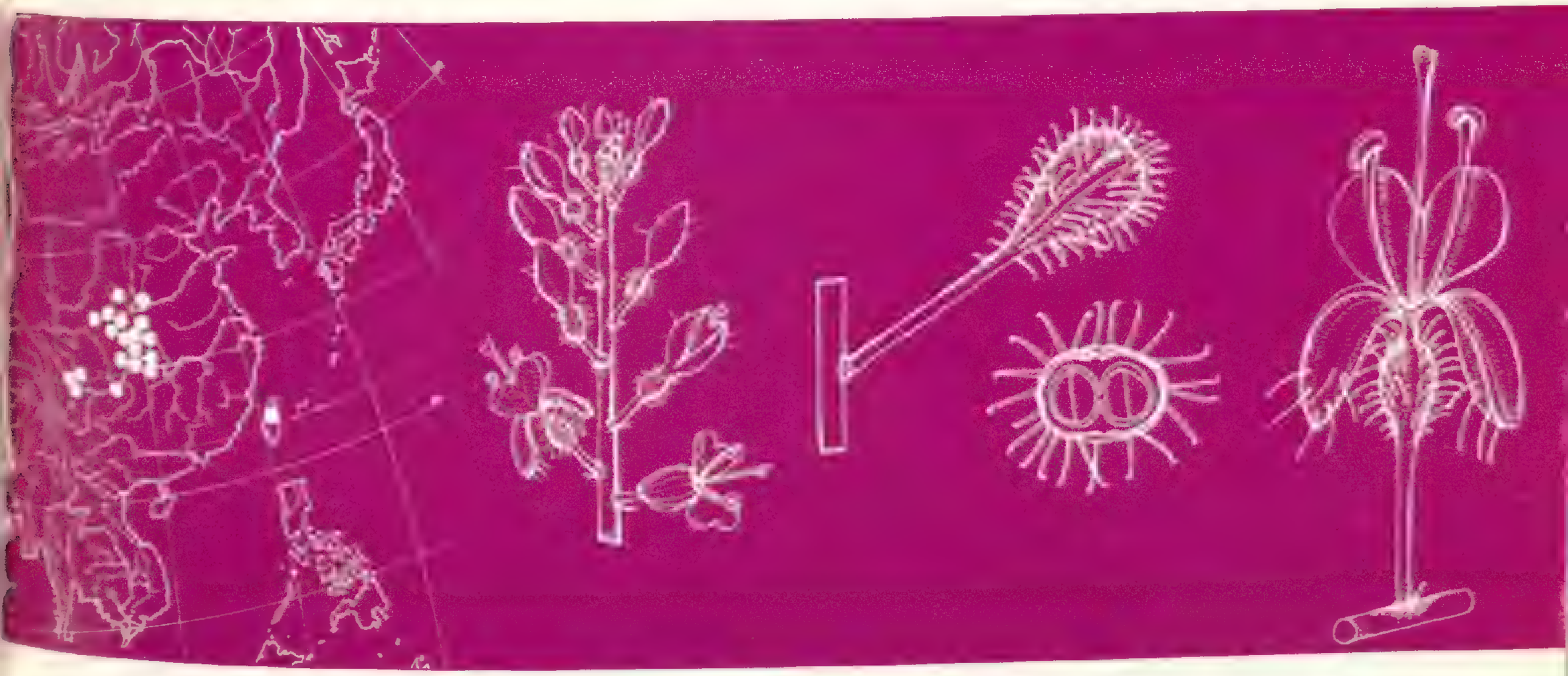

Circaea glabrescens (Pamp.) Hand.-Mazz.

STUDIES IN ONAGRACEAE

CONTENTS

Evolution and Systematics of the Onagraceae: Floral Anatomy — *Richard H. Eyde* 735

Starchy and Starchless Pollen in the Onagraceae — *H. G. Baker & I. Baker* 748

Wood Anatomy of Onagraceae: Further species; root anatomy; significance of vestured pits and allied structures in Dicotyledons — *Sherwin Carlquist* 755

The Evolution and Systematics of Onagraceae: Leaf Anatomy — *Richard C. Keating* 770

The Systematics and Evolution of *Circaea* (Onagraceae) — *David E. Boufford* 804

NOTE:

Nomenclatural Corrections in the Genus *Camissonia* (Onagraceae) — *Peter H. Raven* 995

Index 996

VOLUME 69
1982
NUMBER 4

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OF THE
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EVOLUTION AND SYSTEMATICS OF THE ONAGRACEAE: FLORAL ANATOMY[1]

RICHARD H. EYDE[2]

ABSTRACT

Analysis of floral structure in all onagraceous genera—with *Lopezia* and *Ludwigia* studied most intensively—indicates that the earliest onagrads were isomerous and diplostemonous and had more than four appendages in each whorl. Deeply cleft placentas bore more or less 2-seriate ovules as in *Hauya* and some fuchsias. The ovary was superior within a floral cup that probably varied in prominence from species to species. The nectary was at the junction of cup and gynoecium as in some modern Lythraceae. These old onagrads gave rise to two lines. One line, surviving today as *Ludwigia*, specialized early for wet conditions and higher ovule number. The ovary became inferior with the (minimal?) floral cup disappearing *pari passu* and the nectaries migrating to the ovary's summit; there was no floral tube beyond the ovary and no link with a particular pollinator. A double-barreled vascular supply evolved along with *Ludwigia*'s massive placentas. In the main onagraceous line the inferior ovary evolved independently and without a dual supply. Eventually coevolution with long-tongued pollinators changed the floral cup to an epigynous tube with nectariferous tissue on the tube side of the tube-gynoecium junction. The tube was then lost in certain derivatives of the main onagraceous line: *Gayophytum*, *Gongylocarpus*, *Lopezia*, *Epilobium* sect. *Chamaenerion*, and some circaeas. Some features of onagraceous flowers merit our attention because they may illuminate problems of floral evolution in families unrelated to the Onagraceae. One such feature is the commissural stigma of *Clarkia* and *Epilobium*. *Gayophytum*'s gynoecial vasculature is another.

I first looked into onagraceous flowers because I wanted to understand a peculiarity—transseptal ovular bundles—in an unrelated group (Eyde, 1967). I had learned from the striking diagrams of Baehni and Bonner (1948; Bonner, 1948) that many of the onagrads also supply their ovules via the transseptal route rather than the familiar central route, and I thought there might be transitional forms in the family to aid in explaining this. That is, I hoped that some of the onagrads would turn out to be intermediate for the trait and that the intermediates would show something about the evolution of transseptal vasculature from an ancestral central system.

In time, I learned Baehni and Bonner had not been the first to find transseptal

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[1] The National Science Foundation helped indirectly with grants to P. Raven that supported the field work of several collectors. Photographs are by V. Krantz, drawings by A. Tangerini.

[2] Department of Botany, Smithsonian Institution, Washington, D.C. 20560.

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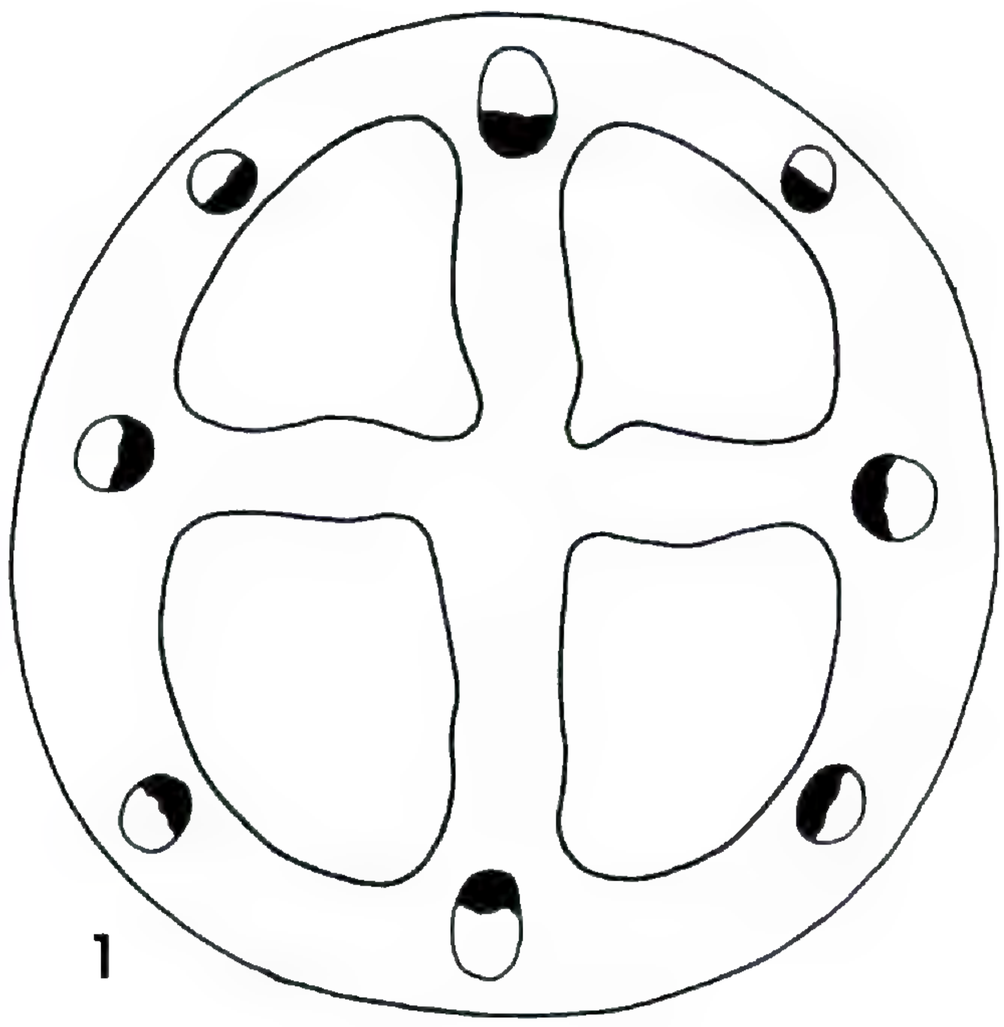
bundles in the Onagraceae. Indeed, Van Tieghem (1868, 1875) illustrated the trait in his prize-winning work on gynoecial vasculature (Figs. 1–4). I learned, too, that although the trait occurs in every genus of the Onagraceae, no genus shows the transition I had envisioned, a central supply going over to a transseptal supply. *Ludwigia* does have a dual system, central and transseptal, in almost every species, but there are several lines of evidence to mark *Ludwigia* as an early offshoot with traits of its own rather than a repository of transitional traits (Eyde, 1981).

Ludwigia's special features include the massive, highly ovuliferous placentas found in species that are on other grounds closest to *Ludwigia*'s ancestry. Another noteworthy feature is the lack of a floral tube beyond the ovary. Ludwigias are not the only tubeless onagrads, to be sure, but they are the only tubeless onagrads without a constriction or neck between the inferior ovary and the epigynous part of the flower. The oddest trait of all is the way *Ludwigia*'s nectaries are placed. The more archaic ludwigias have four or five or more depressed, hair-fringed nectaries—the number depends on the flower's merism—on the raised roof of each ovary, where they occupy the same radii as the ovary's locules. In other onagraceous genera the nectary is commonly a continuous circular region at the junction of the floral tube and the gynoecium. Or, if the nectary extends above that junction, it is clearly on the junction's androecial side rather than its gynoecial side.

I once tried to use nectary position to link *Ludwigia* with *Lopezia* because flowers of both genera, when cross-sectioned, can show nectariferous tissue alternating with the androecial appendages. Lopezia's nectaries, however, are definitely on the androecial side of the gynoecium-androecium junction. Some sections even show secretory tissue in the base of the single stamen and in that of the accompanying staminode (Eyde & Morgan, 1973: figs. 2f & 6f).

Looking into the literature on nectaries for a model—for a group in which interstaminal nectaries seem to have moved from the gynoecial side of the junction to the androecial side or vice versa—I found none. On the contrary, there are a number of groups in which the nectary's position is constant with respect to the junction. The Caryophyllales are the outstanding example. Zandonella's (1972, 1977) examination of 400 species in this order's 11 families turned up no gynoecial nectaries. All caryophyllalean nectaries are on the androecial side of the junction (Figs. 5–10) except in the Phytolaccaceae, thought to be the archaic family, where the nectary can be at the junction without extending more to one side than the other. The Rosaceae are another group in which the nectary is never on the gynoecium. The rosaceous nectary is part of the floral cup, and apparently it is the evolutionary reason for the floral cup: the cup is an expanded nectariferous surface shaped to hold the nectar for pollinators. Brown (1938: 558) may have been the first to apprehend that. A contrasting list of families with nectaries on the gynoecial side of the junction (some members having them at the junction) would include Acanthaceae, Crassulaceae, Ericaceae, Gesneriaceae, and Scrophulariaceae. Figures 11–14 show flowers with gynoecial nectaries.

The explanation for all this, I think, is that many floral nectaries began phyletically at the junction of the gynoecium and surrounding parts, where mechanical stress could trigger cell divisions (see Lintilhac, 1974; Lintilhac & Vesecky, 1980, on stress and morphogenesis). Selection for increased secretion could then



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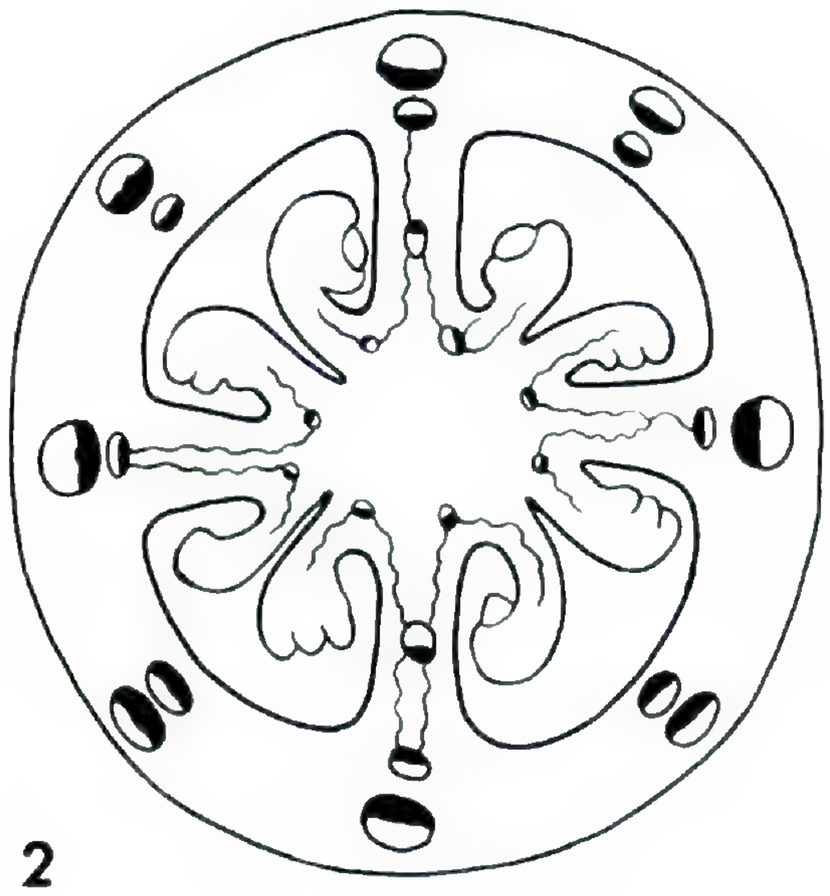

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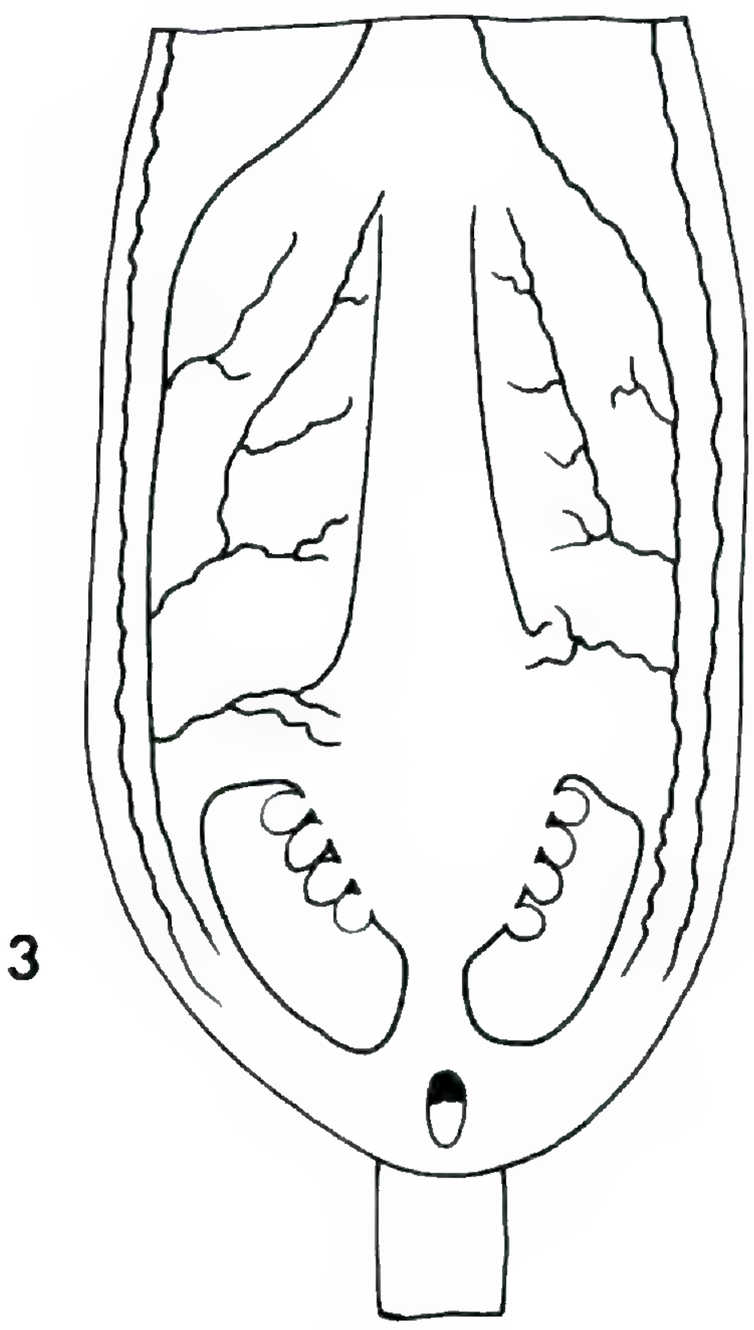

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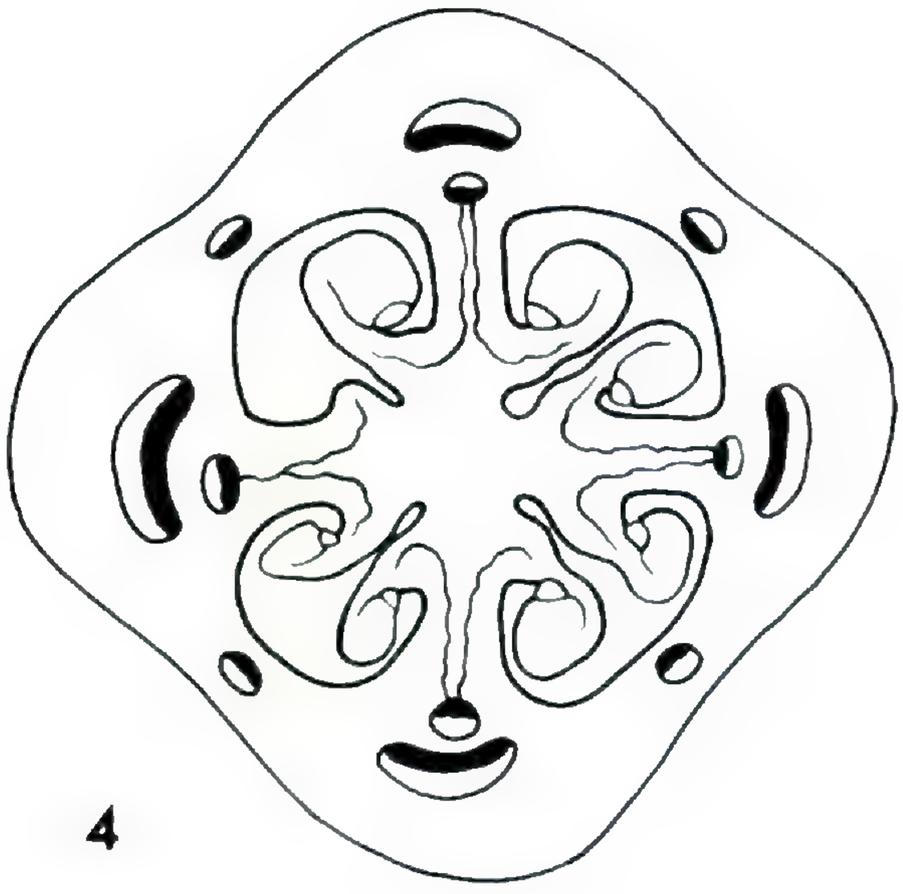

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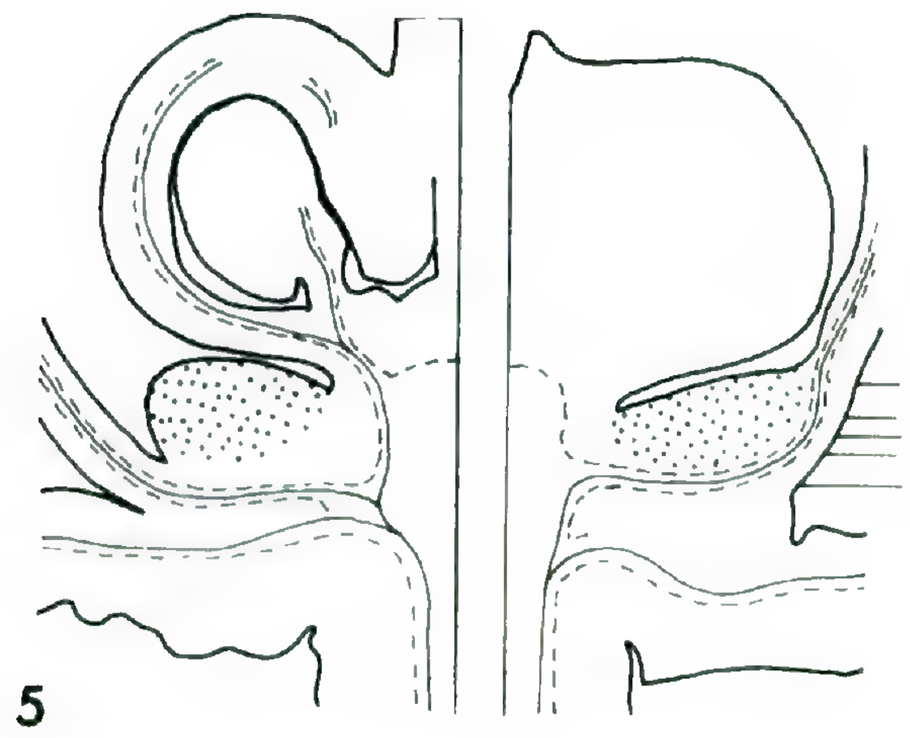
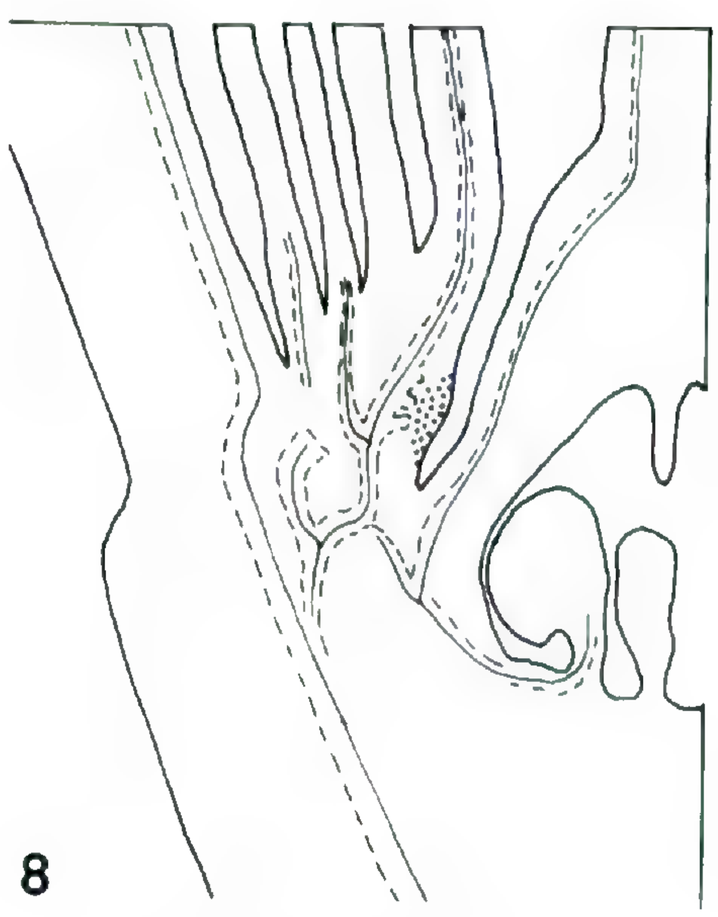
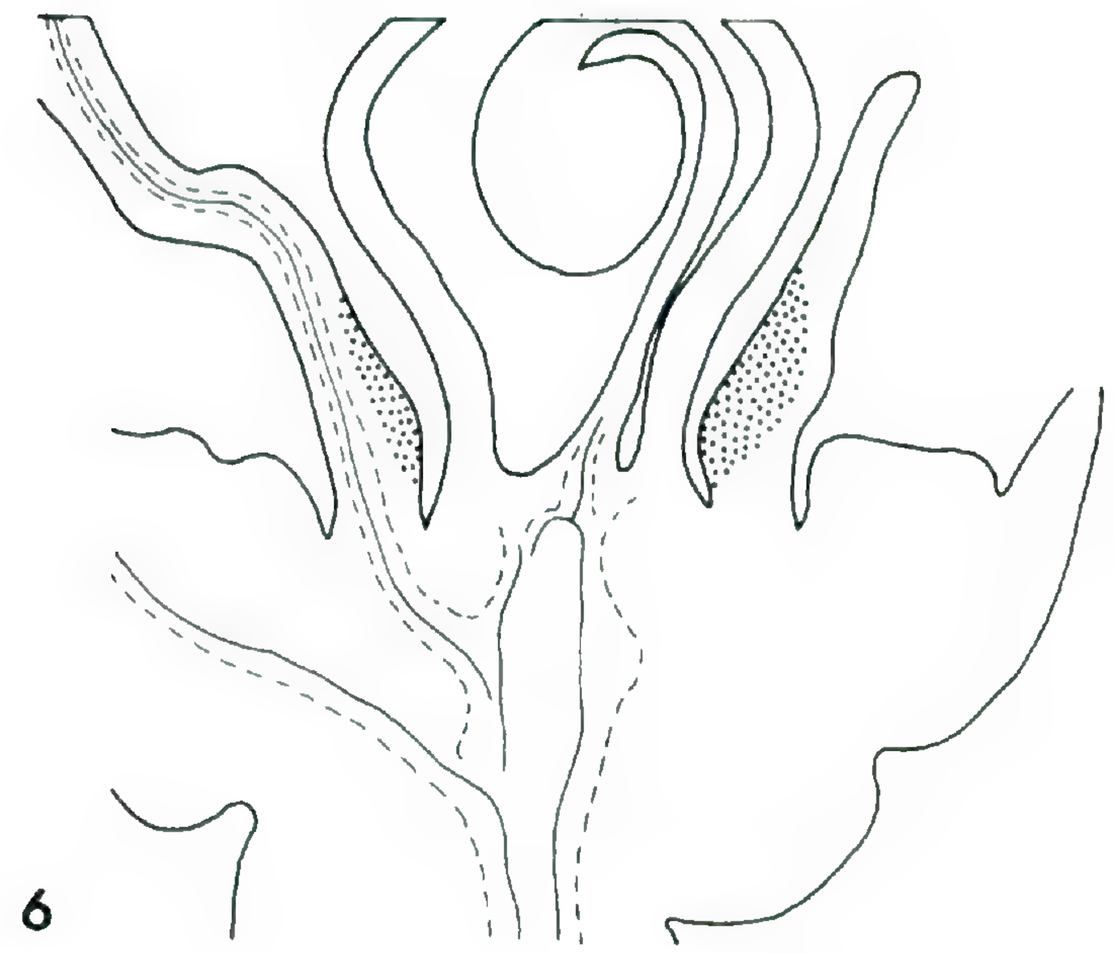
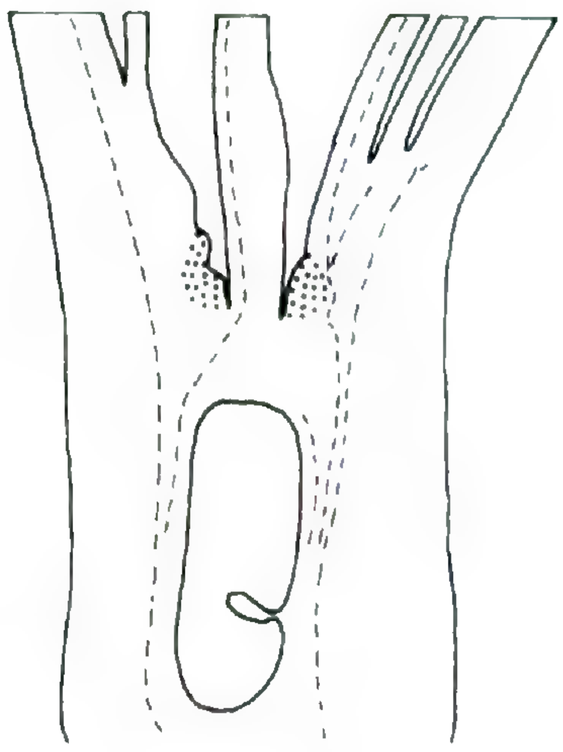
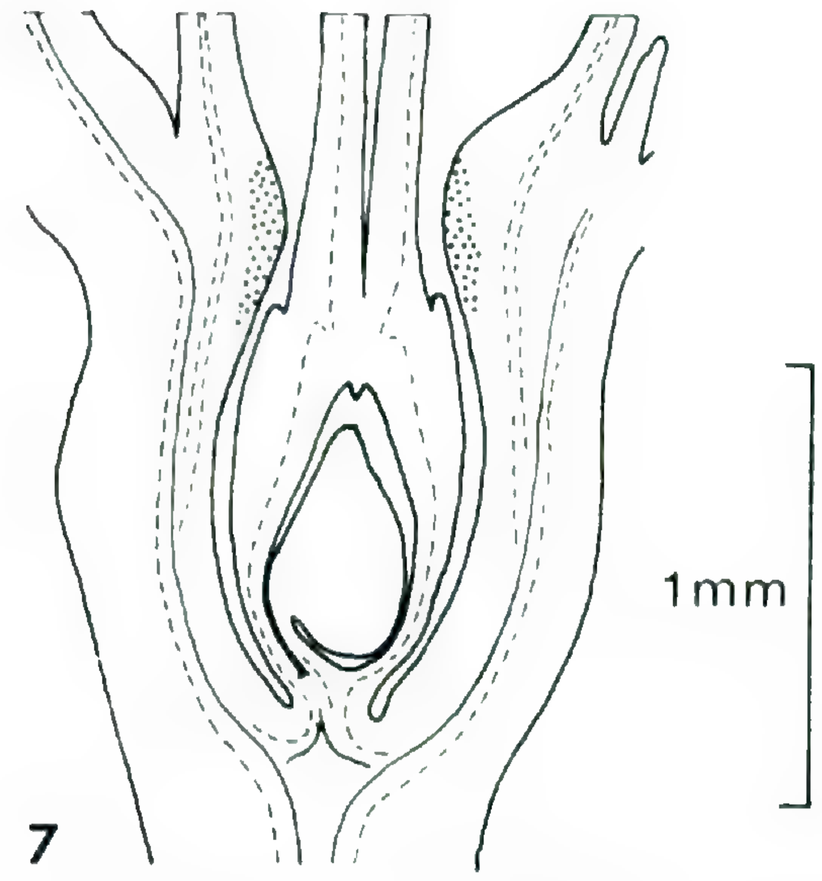
FIGURES 1–4. Four of Van Tieghem's (1875) 13 diagrams of floral vasculature in Onagraceae, redrawn with minor transverse bundles of (inferior) ovary wall left out.—1–3. *Fuchsia fulgens*. Cross sections below ovules and a little above lowermost ovules; longitudinal section through most of two septa and parts of two locules.—4. *Oenothera biennis*, cut a little above lowermost ovules. Longitudinal bundles as well as transseptal bundles supply ovules in Fig. 2, but it is clear from Fig. 3 that these longitudinal bundles are upward extensions of transseptal bundles. Van Tieghem pointed out in a legend that there are no central bundles in the flower's base, and his text (p. 153) called attention to the oddity: "Cette absence de faisceaux longitudinaux dans les bords mêmes des carpelles est une circonstance assez curieuse . . . ."

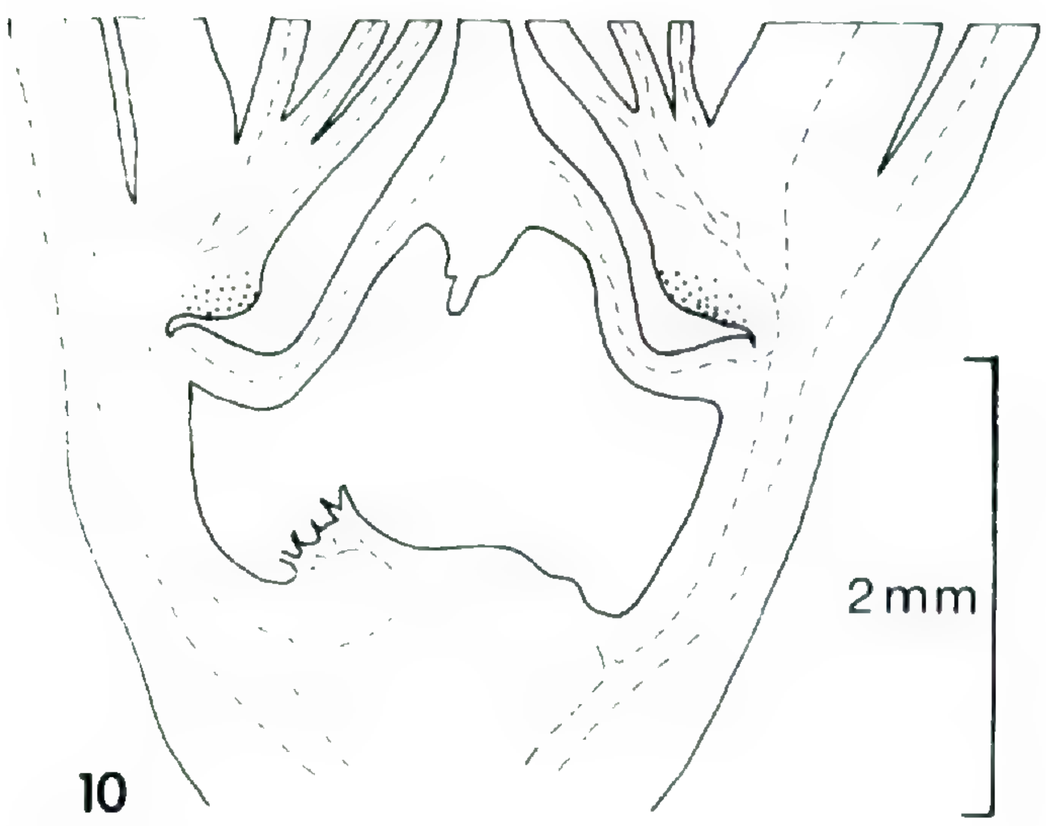




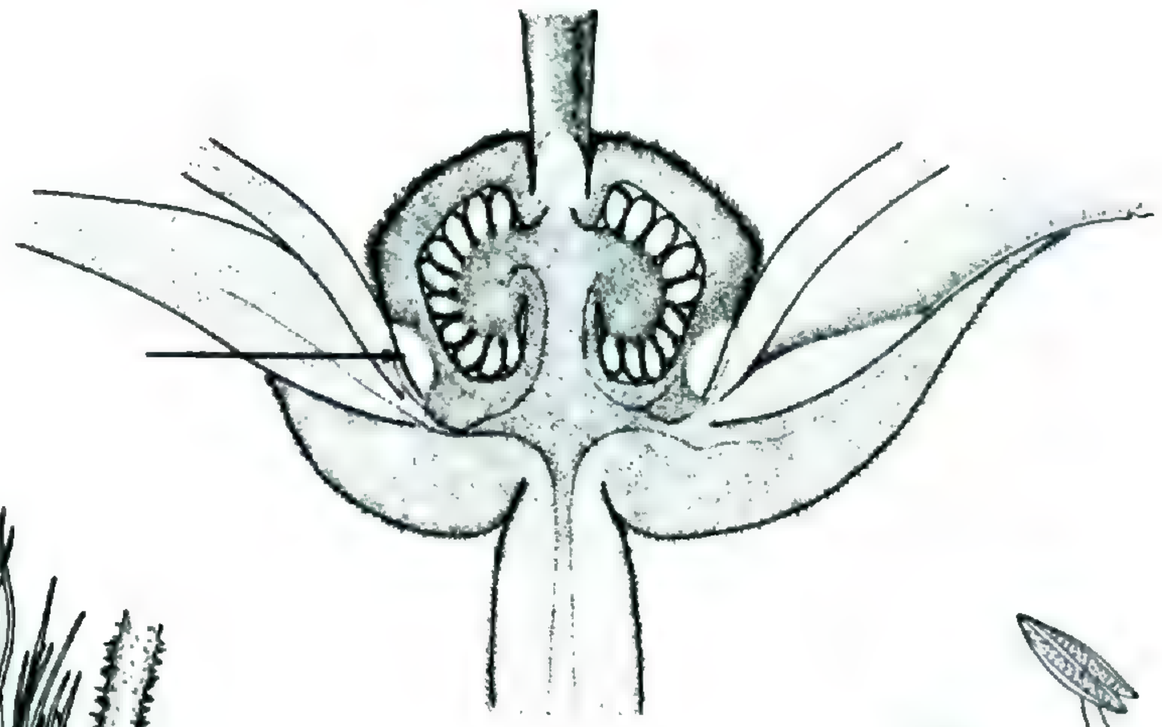








FIGURES 5–10. Diagrammatic longitudinal sections showing androecial nectaries (stippled) in Caryophyllales.—5. *Phytolacca icosandra* (Phytolaccaceae), cut through locule and septum.—6. *Alternanthera sessilis* (Amaranthaceae).—7. *Scleranthus perennis* subsp. *dichotomus* (Caryophyllaceae).—8. *Pereskia diaz-romeroana* (Cactaceae).—9. *Rhipsalis houlletiana* (Cactaceae).—10. *Portulaca grandiflora* (Portulacaceae). All from Zandonella (1972) with permission.



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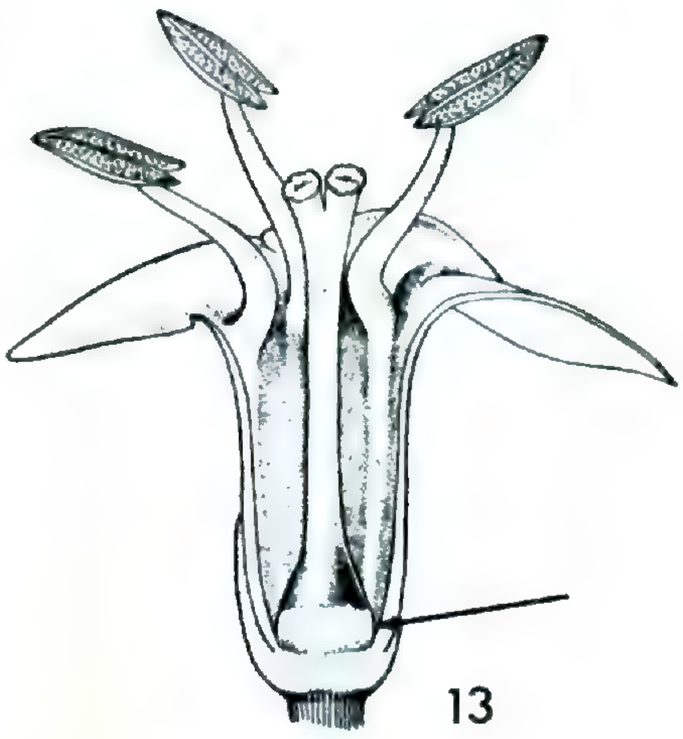

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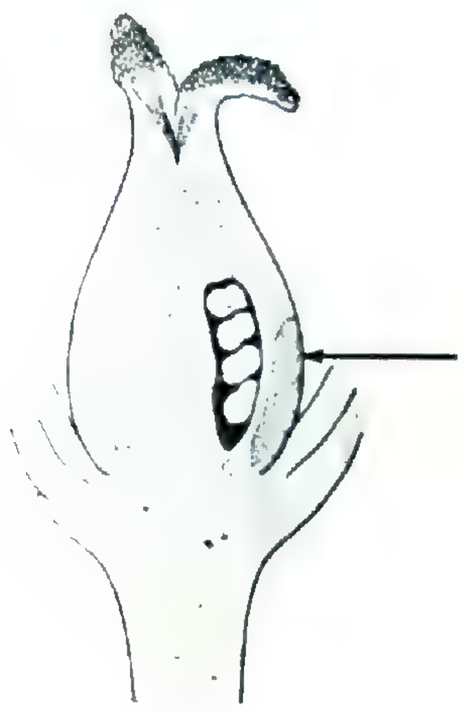

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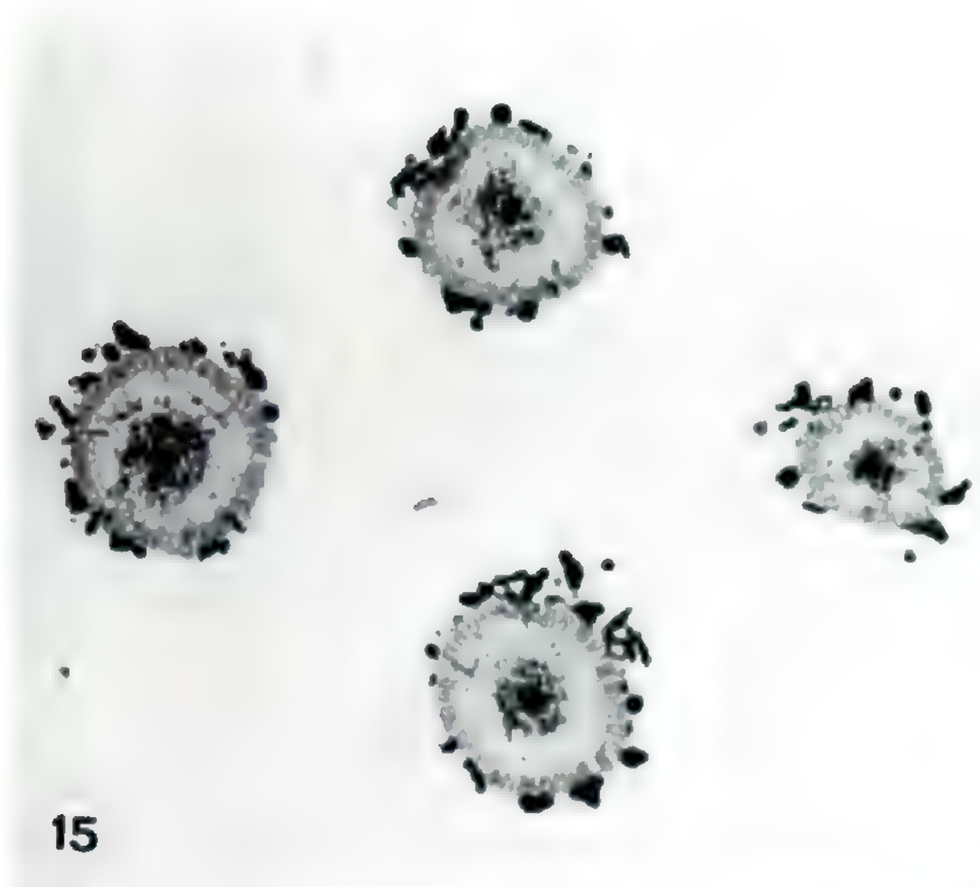
FIGURES 11–14. Gynoecial nectaries (arrows) in members of four families.—11. *Clethra canescens* (Clethraceae).—12. *Rhododendron japonicum* (Ericaceae).—13. *Ehretia navesii* (Boraginaceae).—14. *Eurya japonica* (Theaceae). All from Brown (1938).

enlarge the nectary without moving it, giving it the pulvinate or toroidal form we see in many kinds of flowers. Or such selection could cause the nectary to extend further up one side of the junction or the other. Once the nectary had shifted to one side, it would not easily move back across the notch and up the other side.

To apply this line of thought to the Onagraceae, one must begin before the ovary was inferior, with an ancestral group in which some members had nectaries at the junction, some to one side of the junction, and some to the other, the same sort of diversity in nectary placement still found in the neighboring family Lythraceae. *Ludwigia* evolved from members with nectaries more to the gynoecial side and got the inferior ovary independently of the other onagrads. Transseptal bundles evolved with the inferior ovary in both the *Ludwigia* line and the main line. (They are found here and there among other myrtalean families, too, but only where the flowers are hypogynous.) The gynoecium's old central bundles vanished from the main line, transseptal bundles replacing them completely. In the *Ludwigia* line, however, the central bundles stayed on as the transseptal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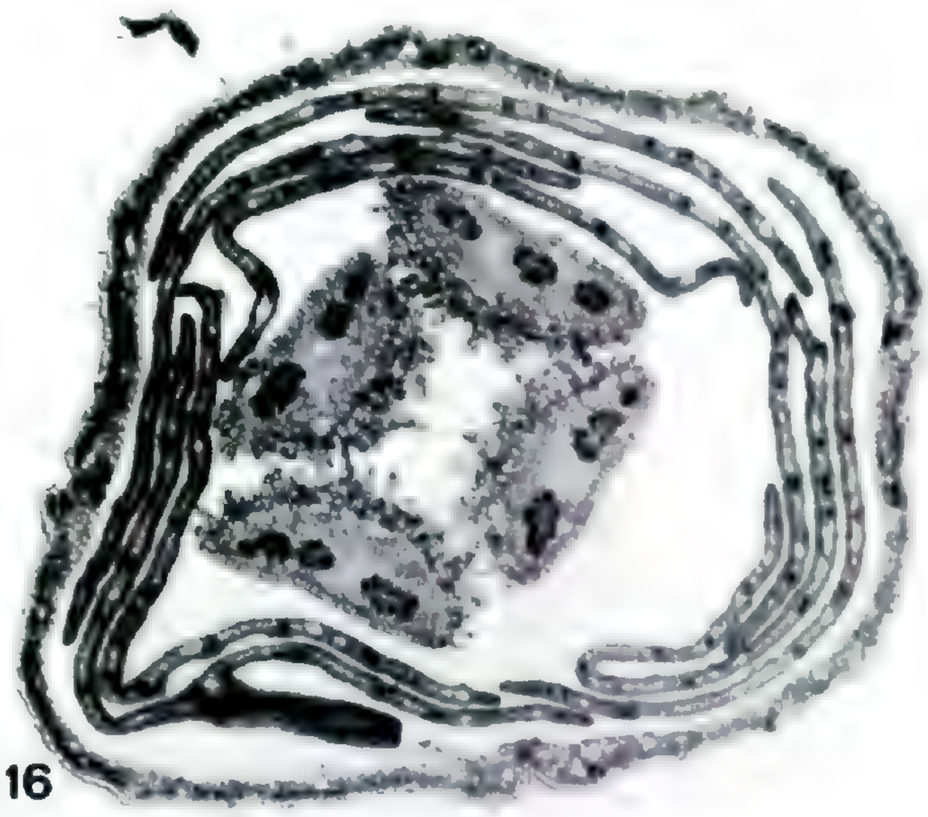
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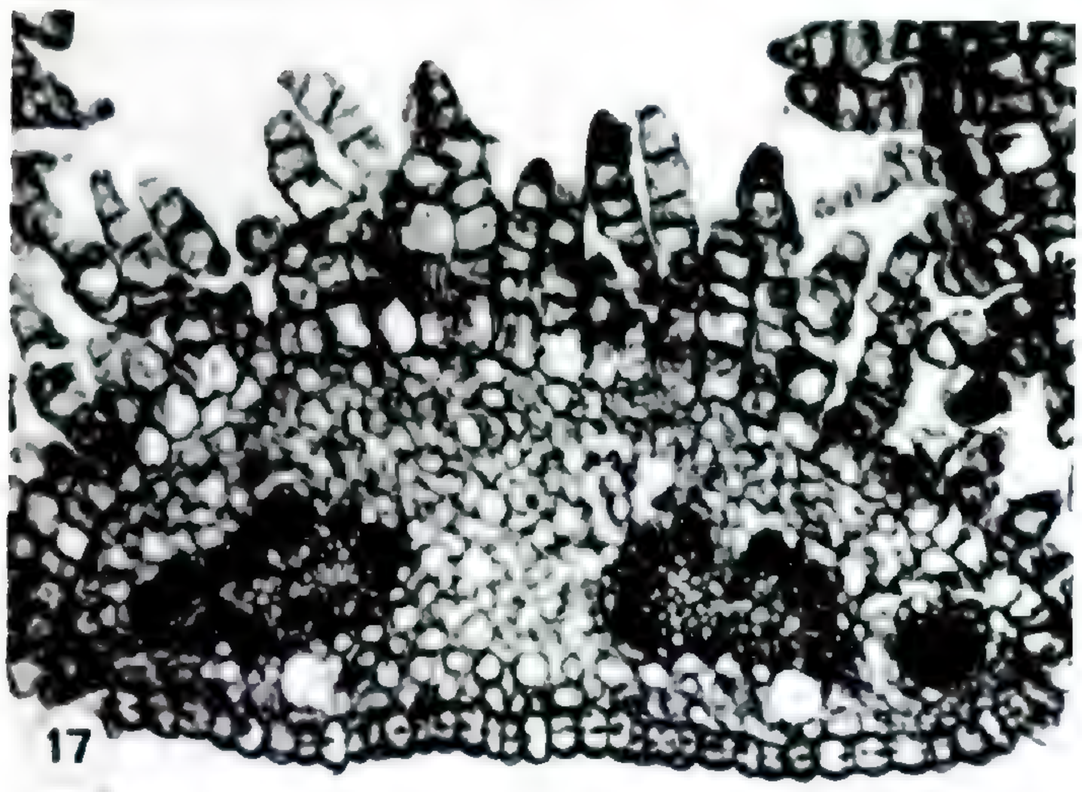
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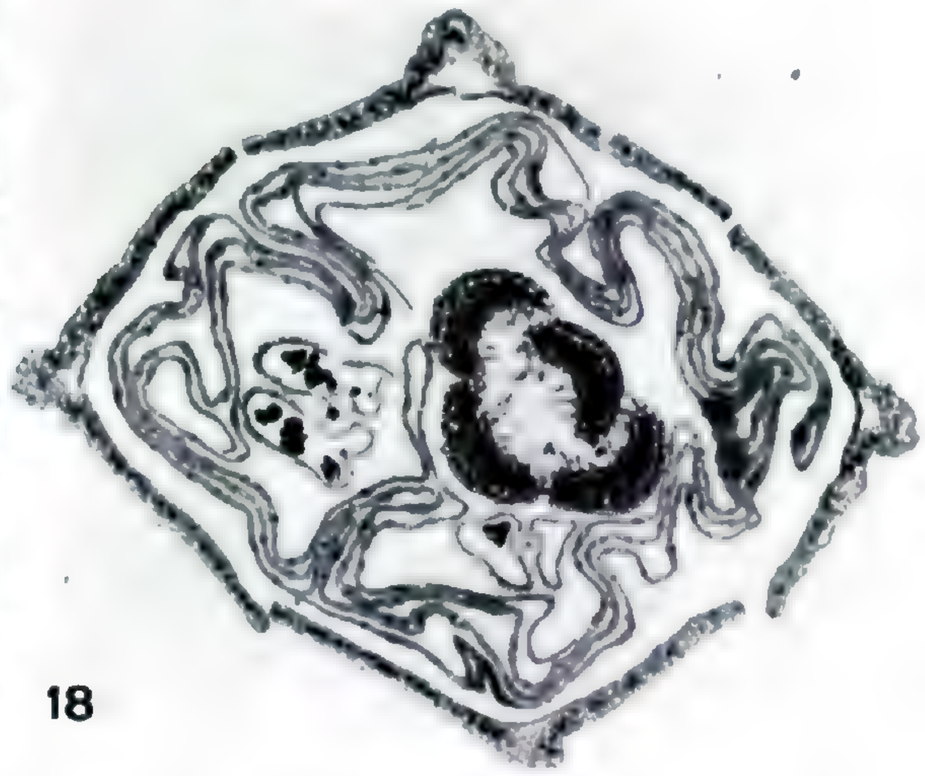
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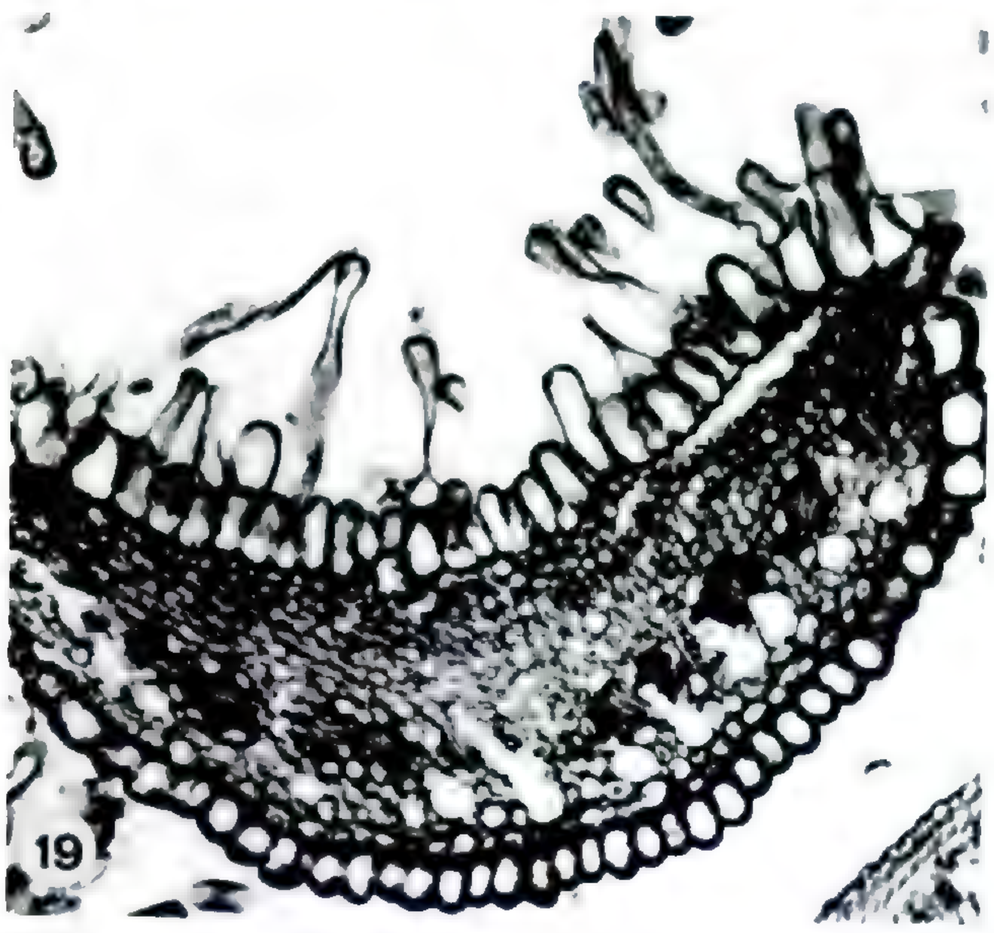
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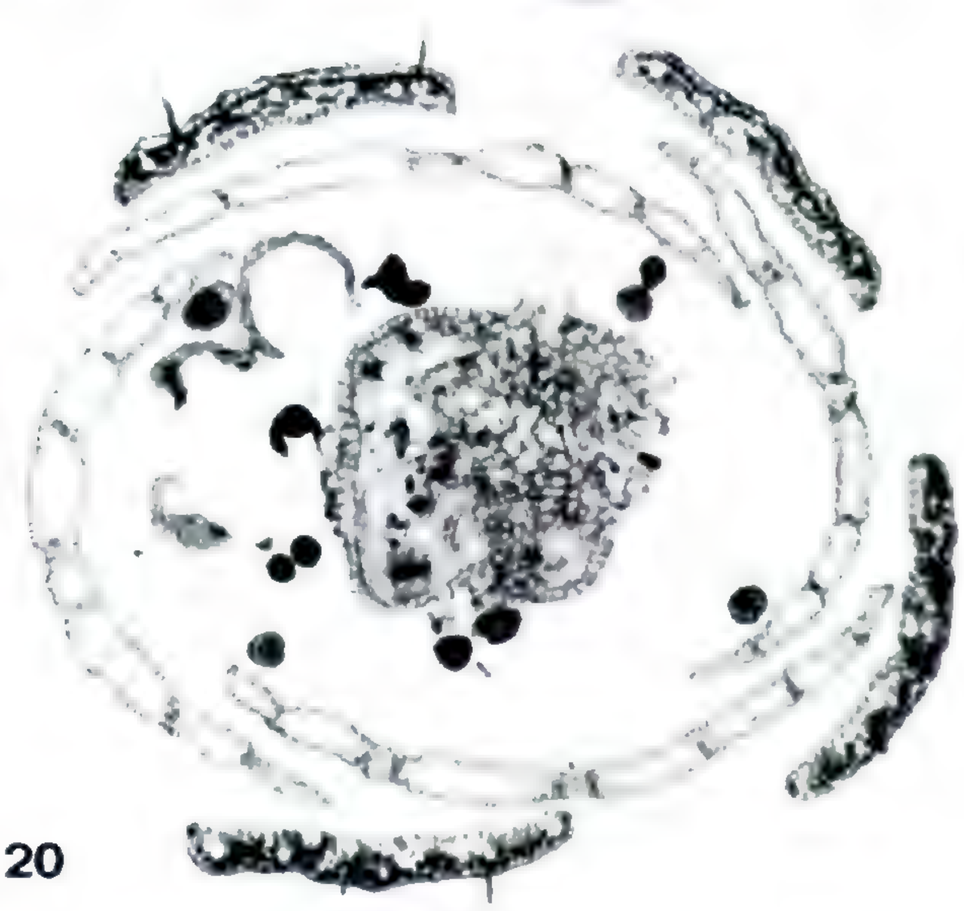
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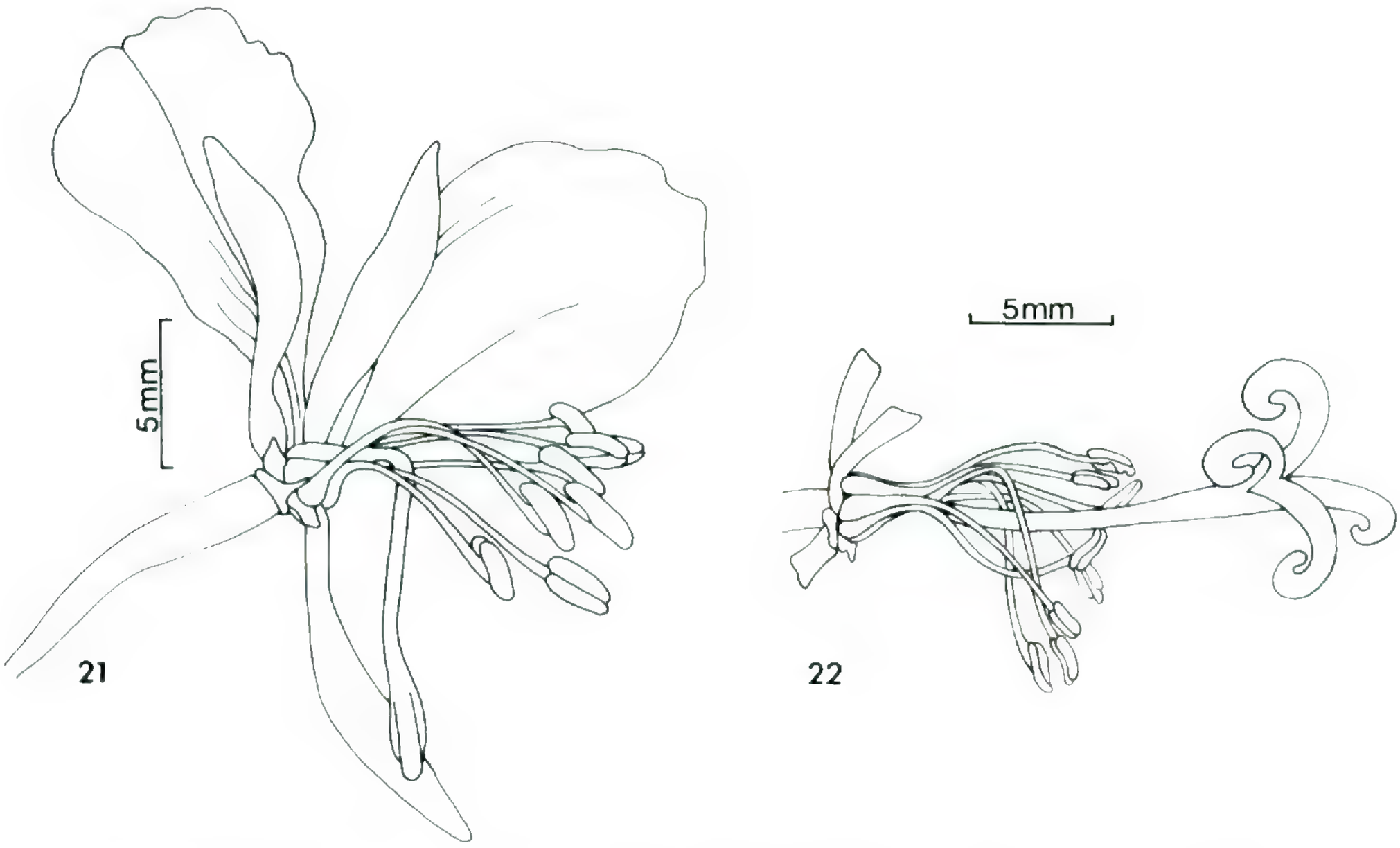
FIGURES 15–20.—15. *Oenothera rosea, Raven 19084* (DS). Cross section through four stigmas showing circular outlines, all-around receptivity. ×27.—16. *Epilobium hirsutum*, cultivated, Missouri Botanical Garden. Cross-section through stigmas showing flatter outline. ×28.—17. Same, one stigma enlarged. Note receptive inner surface modified by cell divisions. ×170.—18. *Clarkia imbricata*, cultivated, University of California, Berkeley. Cross section through stigmas. ×11.—19. Same, one stigma enlarged. Receptive surface has undergone fewer divisions than that of *Epilobium*. ×80.—20. *E. minutum*, cultivated, Missouri Botanical Garden (seeds from *Seavey in 1974*). Section shows pollen germinating on stigma before anthesis. Stigma obscurely lobed in carinal radii. ×47.

supply evolved. Here the double-barreled vascular system tied in adaptively with hypogyny and big placentas: 2-way transport within the inferior ovary sustained more ovules and raised the reproductive rate (Eyde, 1981). *Ludwigia*'s divergence from the main line onagrads was furthered by its early entry into wet but unstable sites where populations that could colonize quickly had a marked competitive edge. Evidence for this can be seen in the wet habitats of today's ludwigias (Ramamoorthy, 1981) and in the widespread occurrence of *Ludwigia*-like pollen in swamp deposits of early Tertiary epochs (references in Eyde & Morgan, 1973; see also Muller, 1981).

Comparisons within the Onagraceae and with selected members of other myrtalean families (Eyde, 1977, 1981) indicate that flowers of ancestral onagrads were isomerous and diplostemonous and had more than four appendages in each whorl. Deeply cleft placentas bore more or less 2-seriate ovules as in *Hauya* and some fuchsias. Around the superior gynoecium was a floral cup that varied in prominence from species to species. Members of the *Ludwigia* line need never have been pollinated by anything but the same sorts of unspecialized insects now pollinating them. Main line onagrads, on the other hand, coevolved with long-tongued insects, and a floral tube was part of the evolutionary package. For the mainliners, the evolution of the inferior ovary may have been just one aspect of an overall reshaping of the flower toward efficient and restricted use by more and more specialized pollinators.

An anatomist must savor the systematic insights gotten from *Ludwigia* flowers because the floral structure of other onagrads is not so instructive. Lately, I have been looking at the commissural stigmas found nowhere in the family but in *Clarkia* and in the Epilobieae—*Epilobium* and *Boisduvalia*. Wherever there are four stigmas (for present purposes the distinction between four stigmas and four stigmatic lobes is one of degree only) in these genera, they are in line with the sepals and the gynoecial septa, not with the petals and locules as is true of other onagrads with cruciform stigmas. This difference is easily overlooked because styles rotate a bit in the bud, but other differences go with the positional differences. *Oenothera* stigmas, for example, are circular in cross section; each has but one big vascular bundle and a smooth epidermis that is receptive all around (Fig. 15). *Epilobium*'s commissural stigmas are flatter structures (Fig. 16), with the upper epidermis modified by division and radial elongation of its cells (Fig. 17). Here the vascular supply consists of plural bundles connecting below with the four main style bundles (Bonner, 1948, fig. 12), which are in the petal radii. The South American endemic *Boisduvalia subulata*, the only boisduvalia with expanded stigmas, has stigmas like those of *Epilobium*; so does *Clarkia* (Figs. 18–19) except that the epidermal cells of a *Clarkia* stigma lengthen irregularly and divide infrequently.

The three genera are constant for the trait in that the stigmas never expand much in the normal (carinal) radii; in general, the style of an outcrosser ends in four commissural stigmas (Figs. 21–22) and that of a self-pollinating species ends in a small, more or less capitate or discoid stigma (Fig. 20). I say more or less because the stigmas of selfers can show lobing in cross-section, but the lobes are so shallow and so variable as to be useless to a taxonomist. I sectioned stigmas from four collections of *Epilobium paniculatum* (pickled material, 2–4 flowers

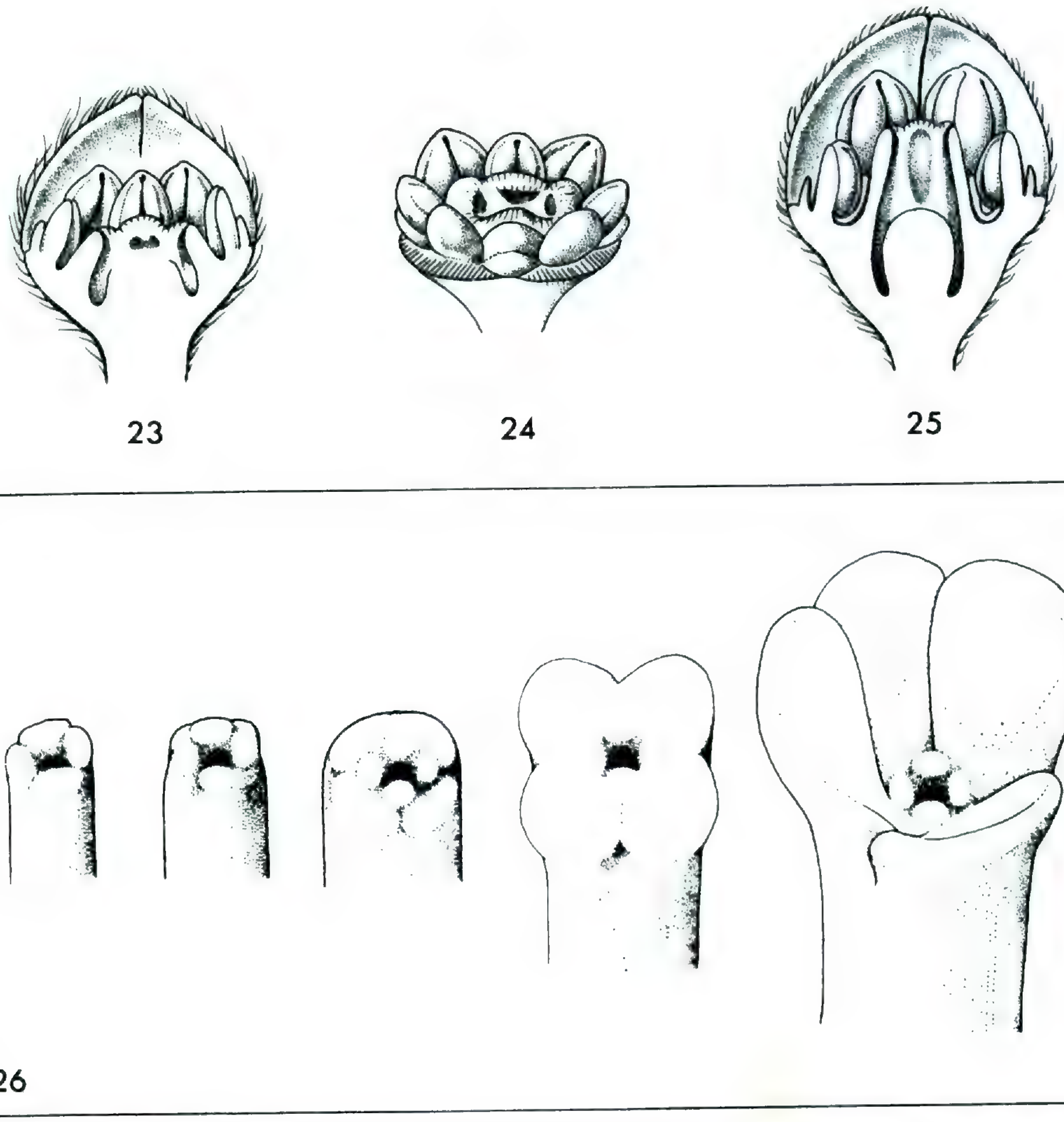


FIGURES 21–22. Protandry in *Epilobium angustifolium*, redrawn from Kartashova (1965).—21. Flower at pollen-shedding stage.—22. Later stage, commissural stigmas receptive to cross-pollination, largely by bees. Barcianu reported the odd disposition of *Epilobium*'s stigmas in 1874, but the observation went unheeded by systematists.

each), and this is what I found: no lobes in *Raven 23000* (DS); slight carinal lobes in *Raven 26465* (MO); slight commissural lobes in two plants cultivated at the Missouri Botanical Garden, one sent to me as *M554*, the other as "seeds from *Seavey 1128*."

Unfair as it may seem to a systematic anatomist, commissural stigmas are a parallel development in *Clarkia* and *Epilobium*, a structural aspect of protandry rather than a mark of shared ancestry, for the genera are far apart on other evidence. Those epilobiums and clarkias that have changed—reverted, I think—from protandry to selfing, have done away with commissural stigmas as part of the change. And if Raven (1979: 591) was right in saying the South American endemic *Boisduvalia subulata* began to outbreed after its forebears arrived in South America, it, too, got its commissural stigmas independently. Commissural stigmas form late in floral ontogeny between the tips of the four gynoecial primordia, tips that would in *Oenothera* lengthen into carinal stigmas. They overtop the primordial tips as the style grows (Kowalewicz, 1956; Mayr, 1969; Figs. 23–27). No doubt this is a reason for the plasticity of commissural stigmas. Arising when the flower bud is fairly well developed, they can be gained or lost without disrupting other developmental events.

Boisduvalia subulata is the only boisduvalia with clearly and constantly divided stigmas. Other boisduvalias have more or less capitate stigmas. The same was true, I think, of the ancestral group common to *Boisduvalia* and *Epilobium*, because a more or less capitate ancestral stigma links the Epilobieae straightaway with the other onagrads: Raven's (1977: 330) 4-lobed ancestors are not needed for the tribe as a whole and would require still earlier ancestors with



FIGURES 23–26. Ontogeny of stigmas in *Epilobium*.—23–25. *E. angustifolium*. Two early stages in floral development, redrawn from Payer (1857). 23 & 24 show same stage; bud is halved in 23, dissected in 24. 25 is later stage. Note gynoecial primordia in carinal radii.—26. *E. hirsutum*. Mayr (1969) drew this sequence of hand lens views showing commissural overtopping of the primordia. Reproduced with permission.

clavate or capitate stigmas to tie the Epilobieae to the rest of the family. The evolutionary history that Raven infers for *Boisduvalia subulata* can serve as a model for the tribe's history except that the scene shifts to North America. I picture the tribal ancestors as a small population; largely self-pollinating but able to outcross; perennial and xerophytic like the more archaic epilobiums but closer to *Boisduvalia* in their floral structure, their coma-free seeds, and their chromosome numbers (here I follow Raven, 1977). Within this population and its descendants enough outbreeding, isolation, and selection took place for *Boisduvalia* to diverge and radiate into the moister habitats that all six species now occupy. Radiation was faster and more effective in the *Epilobium* line because comatose seeds, commissural stigmas, and protandry evolved early and because commissural stigmas remitted rather readily whenever changed conditions fa-

vored modal selfing. In short, I picture the tribe's evolutionary history as more punctuated than gradual and the capitate stigma as a kind of punctuation mark.

Clarkia's history was similar but even more punctuated. Indeed, the genus holds the best based botanical examples of sudden speciation (see Raven & Axelrod, 1978: 82–83; Stanley, 1979: 168, 175). The kinship of *Clarkia* to its nearest neighbor, the monotypic genus *Heterogaura*,[3] differs from the *Epilobium-Boisduvalia* kinship in that there is no need to infer remote common ancestry: the forebears of *Heterogaura* would fit well in *Clarkia*. *Heterogaura* is self-pollinating, to be sure, but its shallow commissural lobes probably came from protandrous precursors.

It is easier to point to a connection between commissural stigmas and protandry than to say how the two are linked. I suspect it is through auxin-induced lengthening of the style, the auxin source being the anthers (see Weinland, 1941, for experimental evidence of this in *Oenothera*). If this is true, there ought to be a consistent timing or structural difference between the androecia of "commissural" species and those of their "capitate" relatives, and I have scanned sectioned flower buds for such differences, but so far without success.

Although the commissural stigmas discussed here are disappointing in that they do not mark a single alliance within the Onagraceae, they do add to our general understanding of the peculiarity. Clearly, Eames's (1961: 244) explanation of commissural stigmas, that they are "the result of the fusion of the lobes of a divided stigma with those of the adjacent carpels," will not work for this family. And it would be interesting to know whether commissural stigmas arose in any other families at abrupt evolutionary turning points, self-pollination going over to outbreeding, as seems to have happened in the Onagraceae.

The gynoecial vascular system of *Gayophytum* is another onagraceous novelty that may aid our overall understanding of floral evolution. All nine species (Lewis & Szweykowski, 1964) have 2-locular gynoecia, but the vascular system is that of a 4-merous gynoecium. Four bundles run through the petal radii of the style and end distally in a globose to hemispherical stigma (Fig. 28). Followed downward into the neck between the inferior ovary and the superior part of the flower (Figs. 29–31), each of the four bundles merges with a bundle leading to a petal and an antepetalous stamen. It is easy to track the four bundles on downward from the neck because the path of each is marked by a narrowing of the ovary wall: in cross sections there is an internal notch and an external notch at each of the four positions (Fig. 32). These bundles are more tenuous than the bundles alternating with them, that is, than the four strands supplying sepals and antesepalous stamens. They are so tenuous, in fact, that I question whether they carry much water and photosynthate. It is clear, however, that they have another

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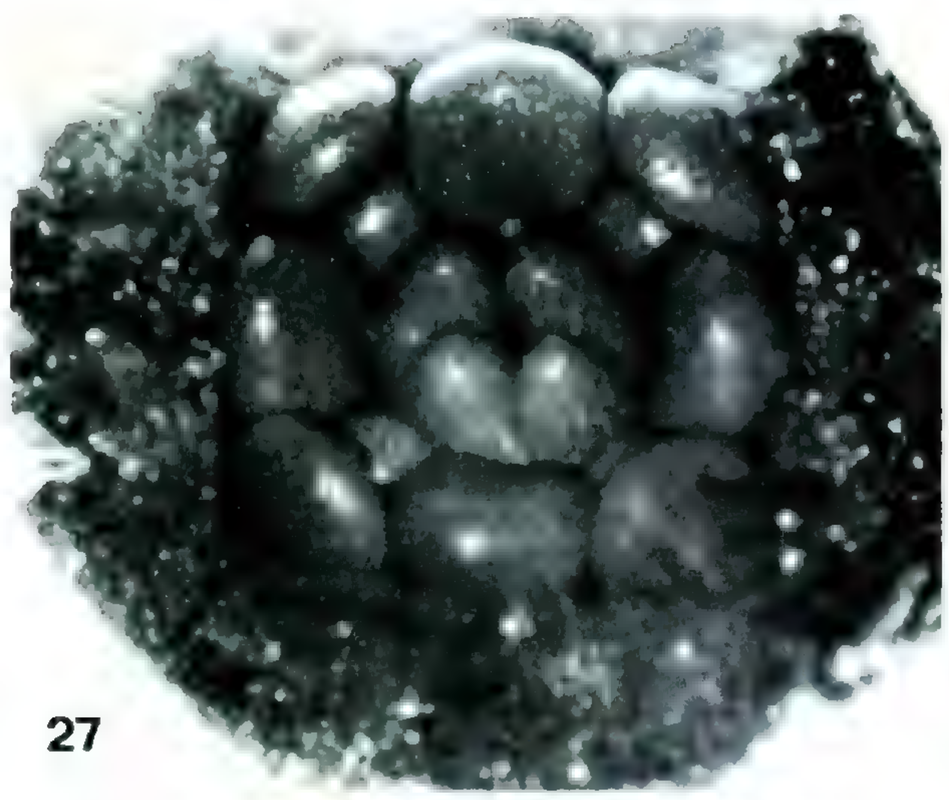
[3] Incongruously, since research on *Clarkia* has gotten to the electrophoretic analysis of genes, simple observations yield new information about *Heterogaura*. I looked at nine serially sectioned flowers from two wet collections—*H. Lewis 1628* (LA), *Gottlieb in 1977* (MO)—and found *Heterogaura*'s gynoecium to be zygomorphic and 2-merous. The ovarian septum is in the median plane, but the two locules lie more to the abaxial side of the flower than to the adaxial, suggesting the phyletic loss of a matching pair of locules from the abaxial side. Sectioned styles show two vascular bundles displaced toward the abaxial side, and the stigma has two shallow, unequal lobes centered in the median (commissural) plane.



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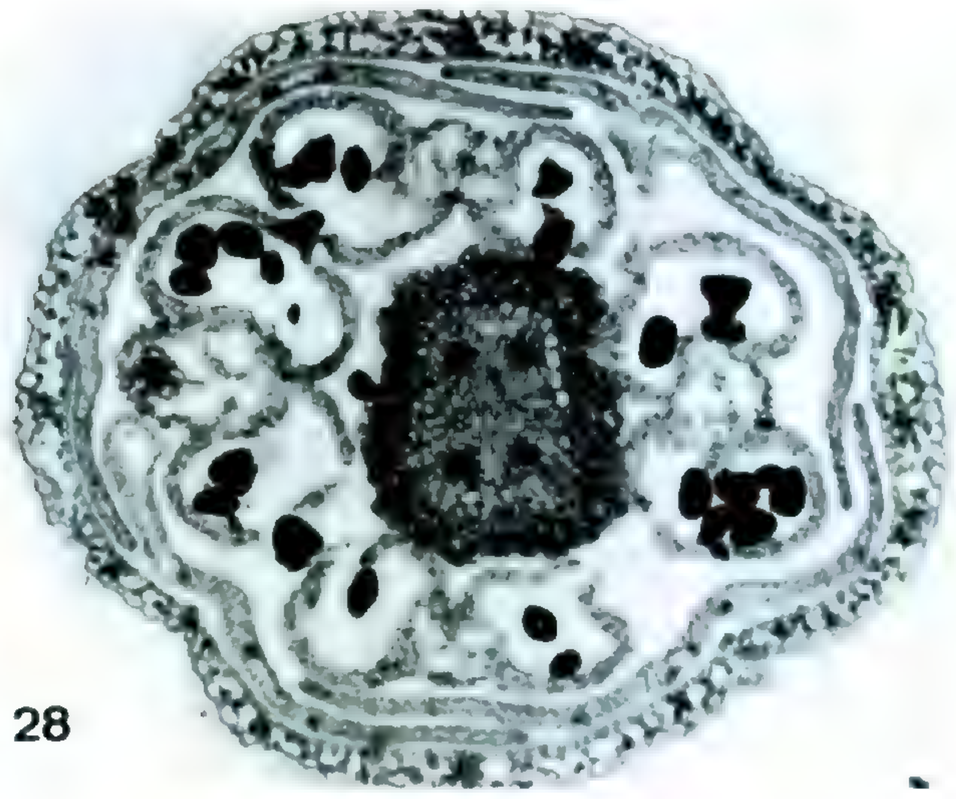

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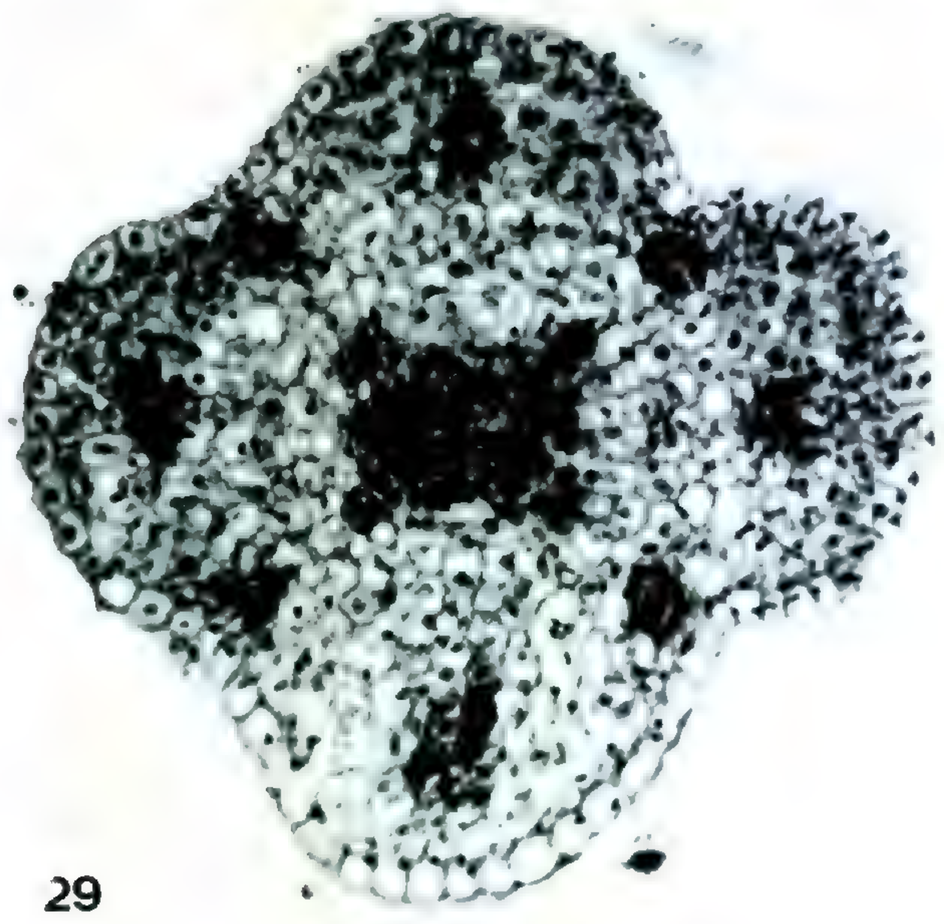

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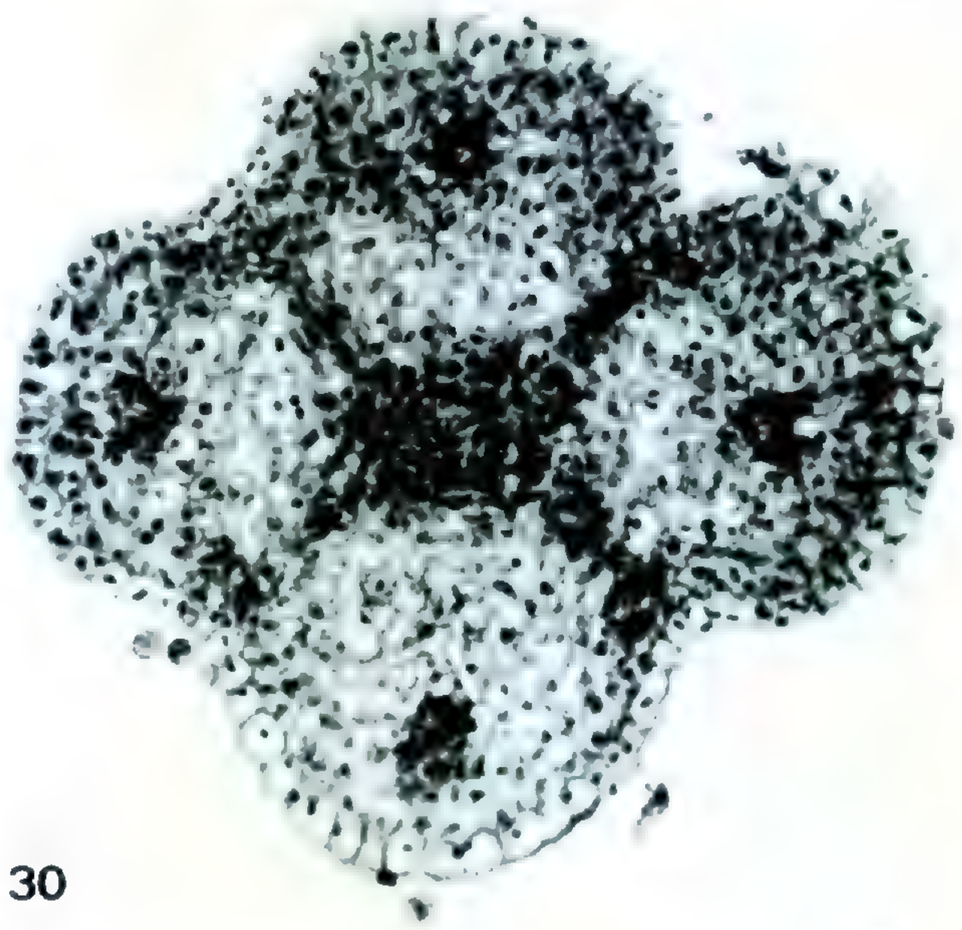

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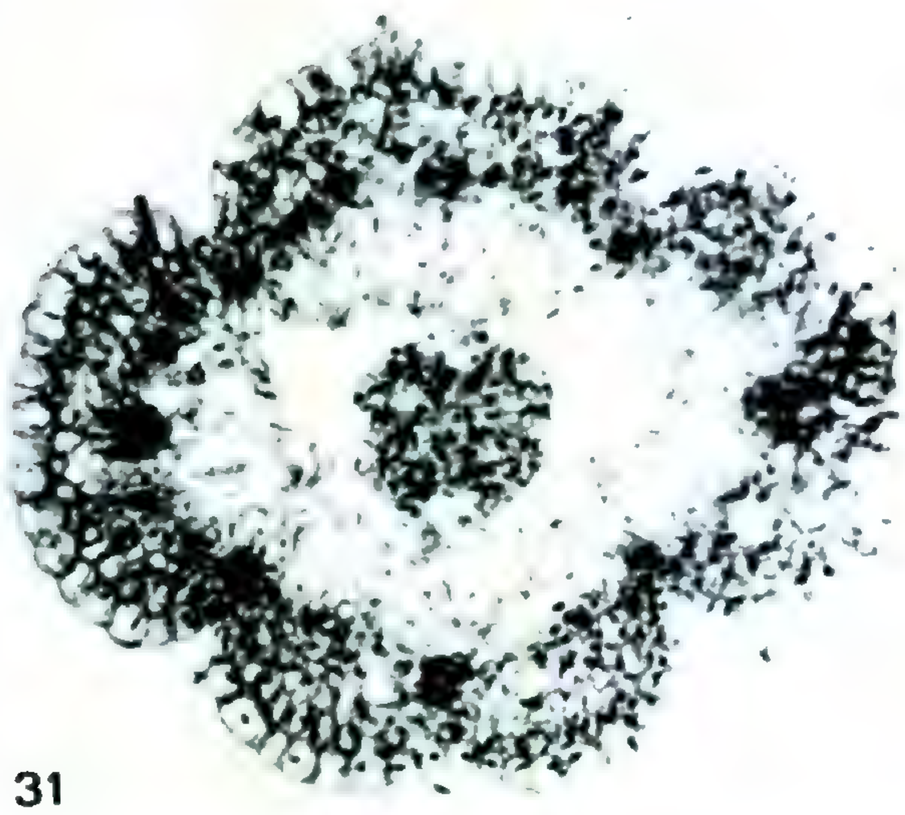

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FIGURES 27–32.—27. Dissected flower bud of garden fuchsia showing four gynoecial primordia at center. Primordia like these become carinal stigmas or receptive lobes in most onagrads but are overtopped by commissural stigmas in protandrous clarkias and epilobiums: see Figs. 23–26. Incident light photo courtesy of R. Sattler (Sattler, 1973: 117). ×85.—28–32. Gynoecial vasculature of *Gayophytum* in cross-section.—28. *G. racemosum, Raven 26420* (MO), cut through stigma to show four bundles aligned with petals. ×54.—29–31. Same collection. Sections from a second flower follow four style bundles basad through epigynous neck to their junction with bundles supplying petals and antepetalous stamens. 29 & 30, ×150, are adjoining sections. 31, ×120, is about 60 μm below 30.—32. *G. diffusum, Seavey 1096*. Four dehiscence lines (darts) in 2-locular ovary are downward extensions of style bundles. Arrows mark sites that the vascular anatomist of yesteryear would call sterile placentas. ×85.

function. Tenuous as they are, these bundles establish weak lines in the ovary wall along which the mature capsule splits. Natural selection has retained them not because of their role in transport but because the freeing and scattering of seeds would go awry without them. With the evolutionary loss of the lateral septa and the evolutionary flattening of the capsule, these four "dehiscence" bundles shifted somewhat toward the transverse plane, further obscuring their origin, in Eamesian terms, as carpel midveins.

As far as I know, *Gayophytum*'s gynoecial vasculature is something new to the literature of floral anatomy, the nearest approximation being in one or another of the pseudomonomerous gynoecia figured by Eckardt (1937; see especially Abb. 25). At first glance, cross sections of a *Gayophytum* ovary bring to mind the crucifer gynoecium, subject of so many wrangles among morphologists. Looked at more closely, the *Gayophytum* gynoecium is quite unlike a real crucifer gynoecium or any morphologist's diagrammatic version of a crucifer gynoecium. A formal, Eamesian interpretation of *Gayophytum* would delineate four carpels, their midveins (darts in Fig. 30) placed diagonally with respect to the pedicel and bract. There would be sterile placentas in the transverse plane (arrows in Fig. 30), but no solid carpels anywhere. In contrast, Eames's interpretation of the crucifer gynoecium (Eames & Wilson, 1930; Eames, 1961) put carpel midveins in the median and transverse planes: those in the median plane belong, he said, to solid carpels. In Eames's view a dehiscing crucifer carpel splits where the solid carpels join the other pair, not along the midveins as in *Gayophytum*. Although Saunders's (1923, 1937–1939) ideas on gynoecial evolution were far from Eames's, her arrangement of crucifer carpels was the same. Indeed, anyone trying to diagram crucifer carpels in another position would come a cropper on *Rorippa barbareifolia* (Stuckey, 1972: 380), a species with four fertile locules, two centered in the median plane and two in the transverse plane. I could go on to give my own interpretation of the crucifer gynoecium—the only good and true one, of course—but we are here to talk about the Onagraceae, and my revelations on that family are enough for one symposium.

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STARCHY AND STARCHLESS POLLEN IN THE ONAGRACEAE

H. G. BAKER[1] AND I. BAKER[1]

ABSTRACT

Mature pollen from 76 species in the complete roster of genera in the Onagraceae was examined for starch-containing or starchless contents. *Fuchsia* and *Lopezia* pollen grains, after passing through a stage of starch accumulation, lose the starch (presumably converted to lipid) and are classified as "starchless." All other genera have pollen that is starch-containing at maturity. The phylogenetic implications of this are considered. Pollen grain diameter is larger in the "starchy" taxa than in the "starchless" ones. There is a strong correlation of pollen grain diameter and the length of style to be traversed by the pollen tube in species with "starchy" grains.

The presence of abundant starch grains in pollen grains of species of *Oenothera* has been appreciated since the 19th century, and Renner (1919a, 1919b, 1921) showed that the size and shape of the starch grains may give a visible expression of the gene-complexes in those species of *Oenothera* that are "complex heterozygotes." We have reported (Baker & Baker, 1979) that there are families of angiosperms that are characterized by starchy pollen grains (e.g. Gramineae, Geraniaceae) and families in which starch does not occur at the time of anther-dehiscence (e.g. Compositae, Cruciferae), but also there are families in which both "starchy" and "starchless" taxa are found. The Onagraceae is one such family.

The purpose of the present paper is to report upon a survey of the pollen reserves of species in all the genera of the Onagraceae and to consider its adaptive and phylogenetic implications. Of great assistance in this is the availability of a comprehensive survey of the reproductive biology of the family by Raven (1979). The family consists of 17 genera in 7 tribes, with about 674 species (Raven, 1979), and we have been able to study the pollen of some species in each of these genera.

MATERIAL AND METHODS

Live floral material was collected in nature in California, England, and Wales, as well as from cultivated plants in the University of California Botanical Garden, the East Bay Regional Parks Botanic Garden (Contra Costa County, California), and the Strybing Arboretum (San Francisco). Particularly valuable was the supply of fresh material of hard-to-get species by Dr. Peter H. Raven, from the Missouri Botanical Garden, and by Dr. James Estes, of the University of Oklahoma. Herbarium specimens of some of the wild collections are being kept in Berkeley and the various institutions have their own vouchers for material.

Care was taken to sample pollen only from anthers that were freshly dehisced, a procedure which is assisted in the Onagraceae by the tendency of the pollen grains to stick together because of the viscin threads that entangle them (Skvarla et al., 1978). Pollen grains were mounted in iodine dissolved in polyvinyl lactophenol to test for starch on a microscope slide and examined for a period of up to

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one week. The diameters of at least 10–30 grains were measured with the aid of a micrometer eyepiece (1 division = 2.86 μm). Contents of the pollen grains usually extend into the pores, hence with triporate grains one pore was included in the measurement. When the pollen grains are biporate, as in some species of *Fuchsia*, the mean of the long and short diameters was taken, so that effectively it was the body and one pore. Where the grains are shed in tetrads only the individual grains were measured. "Bad" pollen grains (misshapened or lacking in contents) were noted but not measured. Then, the pollen grains were squashed by gentle pressure on the coverslip, so that the contents exuded into the test solution. This gave a further opportunity of observing starch in small quantity. The presence of globules of oil (originally external or internal) was recorded and the identity of the globules as lipid confirmed where necessary by staining with Sudan IV.

Observations were also made, when possible, of the pollen in various immature stages as well as at maturity.

In a previous survey of many families (Baker & Baker, 1979) it was noted that larger pollen grains tended to be found in flowers with longer styles although no actual measurements of style-length were made at that time to establish a regression. Consequently, for this study, styles were measured on available material. The interest of this was not appreciated initially and it was necessary in some cases to use herbarium material of the species in question that had already been examined as fresh material to acquire measurements of style length. The measurements made were from the middle of the stigma to the top of the ovary. We realize that the pollen tubes that reach to the ovules at the base of the linear ovary have farther to travel than our measurement but, because of the rapid elongation of the ovary during and after pollination, it was not easy to be sure of the longer measurements.

Results

Starchy and starchless pollen

Observations and measurements of the pollen grains of 76 species in all of the genera are listed in Tables 1 and 2.

All taxa, with the exception of *Fuchsia* and *Lopezia*, were positive for the presence of starch in pollen grains at anthesis, often in large amounts (Table 1). Although *Fuchsia* and *Lopezia* are designated "starchless" at maturity, a few pollen grains containing a small amount of starch may occur. In tracing the development of these pollen grains it was seen that in all taxa there is a sequence of stages, beginning in very young grains with a starchless condition, followed by an accumulation of starch with, in the cases of *Fuchsia* and *Lopezia* only, a final stage before anthesis of the conversion of starch into lipid. As an example, these stages are associated with anther development of *Fuchsia magellanica* in Table 3.

Pollen diameter and starchiness

There is a great range of pollen grain diameters in the family, from 37.2 μm in *Fuchsia thymifolia* to 194.5 μm in *Oenothera caespitosa*. However, the gen-

TABLE 1. Species with pollen containing starch.

	Diameter of Pollen Grains (μm)	Style Length (in mm)
Tribe Jussiaceae		
Ludwigia		
curtisiae	42.9	1.5
octovalvis	77.2	4.0
peploides	77.9	8.0
uruguayensis	105.8	9.5
virgata	57.2	1.9
Tribe Circaeeae		
Circaea		
cordata	45.8	4.3
lutetiana	42.9	4.0
Tribe Hauyeae		
Hauya heydeana	103.0	49.0
Tribe Onagreae		
Gongylocarpus rubricaulis	108.7	4.8
Gayophytum diffusum		
ssp. *diffusum*	82.9	4.0
spp. *parviflorum*	71.5	2.6
Xylonagra arborea	94.4	30.0
ssp. *wigginsii*	95.1	30.7
Camissonia		
angelorum	80.1	11.2
boothii ssp. *decorticans*	94.4	9.1
cardiophylla	123.0	16.5
cheiranthifolia	111.5	9.7
ovata	117.3	10.8
Calylophus toumeyi	128.7	53.1
Gaura		
heterandra	128.7	4.0
parviflora	111.5	3.0
Oenothera		
caespitosa	194.5	154.3
deltoides	124.4	96.0
elata	165.9	64.0
macrosceles	151.6	
organensis	191.6	151.5
pilosella ssp. *sessilis*	157.6	
rosea	94.4	14.0
stubbei	160.2	
Stenosiphon linifolius	94.4	8.5
Clarkia		
breweri	157.3	41.5
concinna	160.2	31.0
deflexa	165.9	19.7
gracilis var. *gracilis*	123.0	10.3
purpurea	120.2	11.1
rubicunda	128.7	19.3
unguiculata	117.3	8.0
williamsonii	140.1	20.8
Heterogaura heterandra	65.8	5.6

TABLE 1. Continued.

	Diameter of Pollen Grains (μm)	Style Length (in mm)
Tribe Epilobieae		
Boisduvalia		
cleistogama	48.6	2.3
densiflora	54.3	4.3
macrantha	91.5	5.3
Epilobium		
alpinum	54.3	4.5
angustifolium	77.2	16.2
brunescens ssp. *brunescens*	58.6	4.1
canum	111.5	37.4
ssp. *angustifolium*	131.6	39.0
ssp. *garrettii*	120.1	
ssp. *latifolium*	123.0	38.4
ssp. *septentrionalis*	108.7	36.8
ciliatum ssp. *ciliatum*	82.9	4.7
glabellum	91.5	
hirsutum	100.1	12.3
hormannii	60.1	4.7
lanceolatum	74.4	6.3
melanocephalum	68.4	
minutum	70.1	2.1
montanum	85.8	7.5
paniculatum	82.9	3.1
?*saximontanum*	65.8	
Mean	102.9	

eralization made for flowering plants by Baker and Baker (1979) holds for the Onagraceae: the mean diameter of pollen grains of taxa that show starchy pollen ($\bar{x}$ = 102.9 μm; range = 42.9 to 194.5 μm; n = 60) is larger than the mean of those with starchless pollen ($\bar{x}$ = 69.0 μm; range = 37.2 to 144.4 μm; n = 16). Standard deviations are not quoted because the data do not have a "normal" distribution. Application of the Wilcoxon two-sample test (adjusted for tied values) gives t_s = 3.174 (d.f. 73) which is significant at the .005 level.

POLLEN DIAMETER AND LENGTH OF STYLE

Tables 1 and 2 also contain the mean style lengths for those species available for the measurement. Analysis of these data for starchy pollen grains (for pollen grain diameter compared with the $\log_{10}$ of style length) by ANOVA showed that the positive correlation is highly significant ($F_{(1,51)}$ = 81.653, where $F_{.001(1,51)}$ = 12.51). Figure 1 shows this relationship for all the species analyzed and the regression line that fits these data. With a correlation coefficient r = 0.785, almost 62% of the variation observed can be explained by this relationship.

A similar analysis for starchless pollen would probably show a similar relationship but insufficient style-length data have been available for statistical investigation.

TABLE 2. Species with pollen not containing starch.

	Diameter of Pollen Grains (μm)	Style Length (in mm)
Tribe Fuchsieae		
Fuchsia		
boliviana	62.9	57.1
collensoi	63.6	
excorticata	62.9	
magellanica	57.2	34.9
microphylla	51.5	
paniculata	45.8	
perscandens	60.1	
pilosa	60.1	
procumbens	57.2	
regia	71.5	
splendens	65.8	
thymifolia	37.2	27.0
Tribe Lopezieae		
Lopezia		
ciliatula	68.6	71.5
langmanniae	124.4	131.6
longiflora	144.4	143.0
racemosa	71.5	
Mean	69.0	

DISCUSSION

As in our general survey of starchy and starchless pollen in a number of families (Baker & Baker, 1979), we find in the Onagraceae that the mean pollen grain diameter of species that produce starchy pollen is significantly greater than that of the species that produce starchless (oil-rich) pollen.

In the same preliminary survey of pollen grains of many families, their contents and their sizes (Baker & Baker, 1979), we drew attention to the significantly larger pollen grains of species with styles longer than 1 cm, compared to those produced by species with styles shorter than this length. However, recently,

TABLE 3. Changes in percentage of pollen grains containing starch in *Fuchsia magellanica* during development.

Stage	Pollen Grain Diameter (μm)	Percentage + (for starch)	Percentage − (for starch)
1. Very young anthers white	52.9	0.7	99.3
2. Anthers with slight tinge of red	54.3	16	84
3. Anthers pale pink	55.8	82.6	17.4
4. Anther wall deep pink; flower not open	55.8	68	32
5. Anthers just beginning to dehisce; flower just beginning to open	57.2	15*	85
6. Open flower	57.2	<1*	>99

* Starch grains that are present are very small.

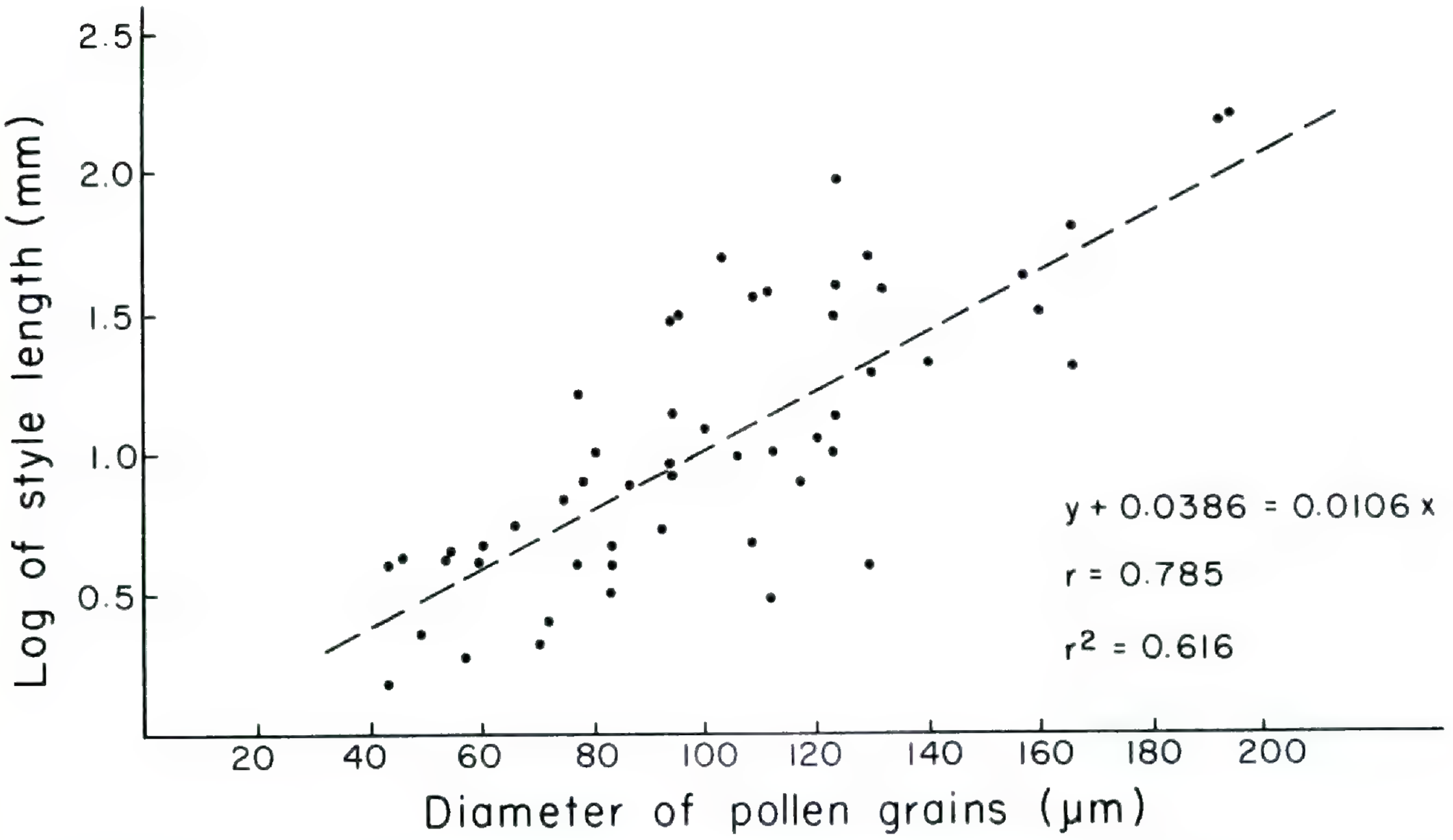

FIGURE 1. Relation of pollen grain diameter and $\log_{10}$ style-length for 53 species with starchy pollen, and calculated regression line.

Cruden and Miller-Ward (1981) have cast doubt on the likelihood that there would be a correlation between pollen grain size and the length of the pollen tube that must be produced to traverse the style from stigma to ovary. They based this belief largely on the supposition that nutrients will be picked up from the style as the tube grows. Undoubtedly, this occurs and, undoubtedly, there is not always a complete correlation between the size of a pollen grain and the amount of "tube-growing" chemicals within it, but, if the species are taxonomically related and if the food reserve is of the same nature, and even if a proportion of the nutrients needed for pollen-tube growth comes from the style, there may be expected to be some correlation of pollen grain diameter with style-length. Our data for 53 onagraceous species (with starchy pollen) show an excellent correlation. The few data relating to starchless grains (*Fuchsia* and *Lopezia*) suggest that a similar correlation, based on smaller diameters overall, would be found.

According to Raven (1979) the genus *Ludwigia* represents a branch at the most primitive level from the Onagraceae stock (see, also, Eyde, 1978, 1979; Raven & Tai, 1979). This offshoot probably occurred in South America. The genus *Fuchsia* also probably had a Southern Hemisphere origin (with South America, again, the probable ancestral home). *Fuchsia* may be the "most generalized" member of the family (i.e. most like the common ancestor of the family, with the exception of *Ludwigia*) (Raven, 1979). *Lopezia* appears to have been developed from the onagraceous stock (i.e. from a common ancestor with *Fuchsia*) when it reached North America. Raven suggests that many subsequent dispersal acts distributed the Onagraceae around the world.

It is difficult to fit the pollen reserves data with these phylogenetic and phytogeographic pictures. Starchy pollen in *Ludwigia* suggests that the ancestral

condition in the Onagraceae was a starchy one (starchy and starchless pollen are both represented in other families of the Myrtales—Baker & Baker, 1979). However, the "starchlessness" of mature *Fuchsia* and *Lopezia* pollen, contrasting with the putatively derived genera of the rest of the family, suggests that starchy pollen is itself a derived condition in the Onagraceae. Starchlessness of *Fuchsia* pollen is not of recent evolution because it is found in the studied representatives of this genus from South and North America and from New Zealand.

No correlation of the nature of pollen reserves with pollinator type is available to explain the starchy or starchlessness of Onagraceae. "Starchless" *Fuchsia* has bird-pollinated, bee-pollinated, fly-pollinated, and butterfly-pollinated species, while *Lopezia* has a similar range of "legitimate" flower-visitors. On the other hand, the "starchy" species of the rest of the family have a range of pollinators that is as wide or wider, including several kinds of moths (Raven, 1979: table 8). Anemophily (wind-pollination), which is frequently associated with starchy pollen (Baker & Baker, 1979), does not occur in the Onagraceae. Autogamy, which is frequently associated with starchy pollen, does occur in many genera and has probably evolved repeatedly (Raven, 1979).

The most likely phylogeny seems to us to specify that the ancestor of the family had starchless pollen but that in *Ludwigia* and in the rest of the family (after *Fuchsia* and *Lopezia* had differentiated) there were switches to "starchiness" by elimination of or restriction of the last stage in the pollen ontogeny, the replacement of starch by lipids. But an explanation of the change on the basis of natural selection cannot yet be given.

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WOOD ANATOMY OF ONAGRACEAE: FURTHER SPECIES; ROOT ANATOMY; SIGNIFICANCE OF VESTURED PITS AND ALLIED STRUCTURES IN DICOTYLEDONS

SHERWIN CARLQUIST[1]

ABSTRACT

Quantitative and qualitative features are described for *Circaea lutetiana* subsp. *canadensis*, *Fuchsia decidua*, *Lopezia suffrutescens*, *Oenothera deltoides* subsp. *howellii*, and six species of *Ludwigia*. Comparison is made between secondary xylem of stem wood and that of tuberous roots for *Fuchsia decidua*; the roots have narrow, angular vessels with scalariform lateral wall pitting in a ground tissue of starch-rich parenchyma indistinguishable from ray cells. Succulent roots of *Xylonagra* show the same features. Wood anatomy for the species studied is interpreted in terms of habit and ecology; features relating to herbaceous modes of structure are discussed since all of the species studied can be termed subshrubs or small to large herbs. A discussion of the systematic distribution of vestured pits is presented. Allied phenomena (warty surfaces in conifer tracheids, warty surfaces in vessel elements some of which are intercontinuous with warts of vestured pits, grooves in vessel walls, and helical thickenings on vessel walls) are considered in conjunction with vestured pits. Experimental data available is minimal, so little evidence other than systematic distribution and occurrence within cell types can be adduced at present. These forms of wall relief seem to occur essentially only in conducting cells. Four hypotheses are entertained: (1), vestured pits as a means of preventing pit membrane rupture in pit aspiration; (2), wall relief as a means of lowering resistance to water flow; (3), wall relief as a mechanism for mending of air embolisms; and (4), wall relief as a means of increasing hydration (bonding of water to wall), thereby enabling high water tensions during drought or frost but lessening likelihood of cavitations. Although all hypotheses are considered possible in terms of today's limited knowledge, the fourth hypothesis is considered the most likely by virtue of systematic, ecological, and cell type occurrence of wall relief types.

Although a large assemblage of woods of Onagraceae have been covered in my two earlier studies (1975a, 1977), the availability of wood of additional species of interest prompts the present study. *Fuchsia decidua* Standl., a shrub of montane (ca. 2,000–3,000 m) Jalisco, Mexico, has semisucculent stems; its roots have swellings that suggest a storage function. This species offers an ideal opportunity to compare stem and root wood, but the roots are of a special type. Although stem wood of *Xylonagra arborea* (Kell.) Donn. Smith & Rose was studied earlier (1975a), liquid preserved material of the tuber-like roots in this plant was available for the present study. These roots offer an interesting comparison with the roots of *Fuchsia decidua*. Woods of *Lopezia* were sampled rather intensively (1975a), thanks to the excellent collections of Dr. Dennis E. Breedlove. One distinctive subshrub, *L. suffrutescens*, is added in the present study. *Lopezia suffrutescens* has numerous stems of short duration (one to several years) branching from the base of the plant. It offers interesting material on which to test the ideas enunciated earlier on the relationships between habit and interxylary phloem presence. *Lopezia suffrutescens* is a species restricted to canyons in Durango and Sinaloa (Plitmann, Raven & Breedlove, 1973).

Six species of *Ludwigia* are included here. The *Ludwigia* species in the earlier (1975a) study lacked interxylary phloem and had relatively mesomorphic

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woods. The species studied here offer material for additional information on these topics. The six *Ludwigia* collections studied here were made in marshy areas of Brazil by T. P. Ramamoorthy and P. M. Vital. Localities are as follows: *L. bullata* (Hassler) Hara, *Ramamoorthy & Vital 609*, Campo Grande, Matto Grosso; *L. elegans* (Camb.) Hara, *R.&V. 535*, Goiania; *L. peruviana* (L.) Hara, *R.&V. 598*, Banderante, Matto Grosso; *L. sericea* (Camb.) Hara, *R.&V. 642*, near Epitacio, Matto Grosso–São Paulo border; *L. tomentosa* (Camb.) Hara, *R.&V. 505*, Paracatu, Minas Gerais; *L.* sp. (aff. *L. longifolia*), *R.&V. 555*, Aereuna, Goias.

Two annuals included in the present study are *Circaea lutetiana* L. subsp. *canadensis* (L.) Asch. & Magnus (Antonia, Jefferson Co., Missouri) and *Oenothera deltoides* T.&F. subsp. *howellii* (Munz) Klein (Antioch, California). The genus *Circaea* has not been studied hitherto with respect to wood anatomy. Both of these annuals show changes in vessel diameter and density (and therefore change in xeromorphy) of wood over the course of a growing season. These patterns invite quantification and application to growth rings in woody plants.

The species included in the present study were assembled and transmitted to me through the kindness of Dr. Peter H. Raven.

The Onagraceae of the present study invite examination of special topics. One of these involves herbaceous modes of structure as exemplified in such respects as ray structure, a low (but not primitive) length ratio of imperforate tracheary elements to vessel elements, and the tendency for pits in walls of vessels to be laterally widened. A second topic of special interest involves vestured pits, which are characteristic of most Onagraceae. Vestured pits, distributed in a scattering of dicotyledon families, have not been easy for plant anatomists to interpret with respect to function. Vestured pits are considered here in a larger context, along with warted vessel and tracheid walls, grooving on vessel walls, and helical thickenings on vessel walls.

The anatomical data offered below for ten species of Onagraceae cannot be applied systematically on account of the fragmentary nature of these data. Those interested in applying wood anatomy to problems of systematics of Onagraceae will have to consult the earlier papers in this series (Carlquist, 1975a, 1977) as well as the summary of Vliet and Baas (1983) of wood anatomy of myrtalean families.

MATERIALS AND METHODS

The species provided to me by Dr. Peter H. Raven were all collected in the wild except for the tuberous roots of *Xylonagra arborea*, which were from a plant cultivated in greenhouses at the Missouri Botanical Garden. The material for this study includes one dried stem, that of *Oenothera deltoides* subsp. *howellii*, collected by Dr. John Thomas. The remaining material was provided in liquid-preserved form, pickled in formalin-acetic alcohol. Although *Oenothera deltoides* subsp. *howellii* had been included in an earlier (1975a) study, study of additional material of this taxon proved desirable. The stems provided of the *Ludwigia* were 1 cm or less in diameter; judging from the size of plants indicated in accompanying data (plants 2–3 m tall in *L. peruviana*, *L. sericea*, and *L. tomentosa*) the material supplied may not represent stems of maximal size for some of the species.

Wood of stems was sectioned on a sliding microtome; sections were stained with safranin. Wood of roots of the *Fuchsia* and the *Xylonagra* was embedded in paraffin; sectioned, without any form of softening, using a rotary microtome; and stained with a safranin-fast green combination; IKI was introduced as a starch stain.

Anatomical Results

Quantitative features are given for the ten species in Table 1. Both quantitative and qualitative features are presented in the descriptions of anatomical categories below and in the discussions of relationship between wood anatomy and ecology and plant habit.

Vessel elements.—The number of vessels per group in the species studied here (Table 1) falls within the range seen earlier in the family. This feature does not show significant variation within the family. Vessel diameter and vessel element length do vary significantly with species and are considered later with respect to ecology.

Vessels are rounded in outline in the species studied (Figs. 1, 11, 12, 15) with the notable exception of root wood of *Fuchsia decidua* (Fig. 6) and of *Xylonagra arborea* (Fig. 5). Vessels in these species are thin walled and narrow in diameter, but they are surrounded by parenchyma cells the same diameter as the vessels or larger. These circumstances probably result in the angular shape, as with species discussed earlier (Carlquist, 1975a, 1975b); within Onagraceae and other predominantly herbaceous families, angular vessels should not be interpreted as primitive.

Lateral wall pitting of vessels shows interesting variations in the present species. In *Circaea* (Fig. 13) and in the various species of *Ludwigia* vessels have pits round in outline, alternately arranged, on intervascular contacts; these two genera have alternate pits, elliptic rather than round, on vessel-parenchyma contacts. In the remaining species of the present study, pitting on vessels might be described as scalariform or pseudoscalariform (Figs. 7, 16). By this latter term I am designating patterns in which an alternate pattern intergrades with a scalariform pattern. Such a pattern is illustrated for stems of *Fuchsia decidua* (Fig. 9), but it was also observed on vessels of *Lopezia suffrutescens*. Vessel-ray contacts in the latter species showed pits with apertures notably wide, or "gaping." *Oenothera deltoides* subsp. *howellii* has all pits on vessels circular in outline.

Vestured pits may be found in all of the taxa presently at hand except *Oenothera deltoides* subsp. *howellii*; vesturing was reported absent in this taxon earlier (Carlquist, 1975a). Even when pits are wide and gaping (Fig. 7), vestures are present in vessels of roots in *Fuchsia decidua*. Possible functional interpretations of vestured pits are offered in a later section of this paper.

Tyloses were observed in vessels of roots of *Fuchsia decidua* (Fig. 7) and in stems of *Lopezia suffrutescens*.

Libriform fibers.—Nucleated libriform fibers occur in all of the species studied here (not visible in *Oenothera deltoides* subsp. *howellii* because that material was dried instead of preserved in liquid). In all of the species studied here, both libriform fibers with gelatinous walls and libriform fibers with ordinary lignified

TABLE 1. Wood characteristics of Onagraceae. (Continued on facing page.)

Species	Collection	1
Circaea lutetiana L. subsp. *canadensis* (L.) Asch. & Magnus	A. Christ in 1975 (MO)	1.68
Fuchsia decidua Standley	Breedlove 15821 (MO)	1.73
Lopezia suffrutescens Munz	Breedlove 24534 (MO)	2.10
Ludwigia bullata (Hassler) Hara	Ramamoorthy & Vital 609 (MO)	1.40
L. elegans (Camb.) Hara	R.&V. 535 (MO)	1.96
L. peruviana (L.) Hara	R.&V. 598 (MO)	1.16
L. sericea (Camb.) Hara	R.&V. 642	1.24
L. tomentosa (Camb.) Hara	R.&V. 505	1.28
L. sp. (aff. *L. longifolia*)	R.&V. 555	1.20
Oenothera deltoides T.&F. subsp. *howellii* (Munz) Klein	J. Thomas	2.11

Legend for Table 1: 1, mean vessels per group. 2, vessels per mm², mean. 3, mean vessel diameter, μm. 4. mean vessel element length, μm. 5, mean libriform fiber length, μm. 6, mean libriform fiber diameter at widest point, μm. 7, mean libriform fiber wall thickness, μm. 8, mean multiseriate ray height, μm. 9, mean uniseriate ray height, μm. 10, ratio of libriform fiber length to vessel element length. 11, vulnerability ratio (vessel diameter divided by vessels per mm²). 12, mesomorphy ratio (vulnerability ratio multiplied by vessel element length). Where more than one figure is shown in columns 2, 3, 11, and 12, the figure before slash = earlywood, figure after = latewood. Means based on 25 measurements.

walls were observed. Gelatinous fibers may be seen above in Fig. 12 and Fig. 15, ordinary fibers below in the same photographs.

Axial parenchyma.—The present species agree with Onagraceae described earlier in having scanty vasicentric parenchyma, limited to a few cells around vessels. However, in roots of *Fuchsia decidua* (Figs. 3, 4, 6) and *Xylonagra arborea* (Fig. 5), axial parenchyma is present instead of libriform fibers. This parenchyma is rich in starch (Figs. 6, 7, 8); some of the grains are compound. The parenchyma cells are much larger in diameter than libriform fibers; longitudinally they are relatively short (Fig. 4) and may represent subdivision of a fusiform initial derivative into perhaps three cells, but the adult cells are not clearly grouped into strands. The axial parenchyma cells in these roots cannot be distinguished from ray cells in a tangential section.

Vascular rays.—Rays in all of the taxa studied here are predominantly uniseriate (Figs. 2, 14, 17). Biseriate or pluriseriate rays are so scarce in some of the taxa that figures for multiseriate ray height were not included for them in Table 1. Ray cells have lignified walls except in the roots of *Fuchsia decidua* (Figs. 3, 4, 6) and *Xylonagra arborea* (Fig. 5). Notably short rays occur in *Oenothera deltoides* subsp. *howellii* (Table 1). Rays consist of upright cells predominantly in all of the species studied except for *Oenothera deltoides* subsp. *howellii*, in which procumbent cells were seen. No square or procumbent cells were seen in rays of *Circaea lutetiana* subsp. *canadensis* (Fig. 14).

Interxylary phloem.—In my 1975a study, the three species of *Ludwigia* studied all lacked interxylary phloem. In the present study, of the six *Ludwigia* species only *L. sericea* has interxylary phloem (Fig. 11). It occurs as bands of various tangential extent near the periphery of the secondary xylem in the stem studied. Relatively large stems were supplied in this species. Interxylary phloem was absent in the collection studied of *Oenothera deltoides* subsp. *howellii*, whereas it was present in a collection of this species studied earlier (Carlquist, 1975a).

TABLE 1. Continued.

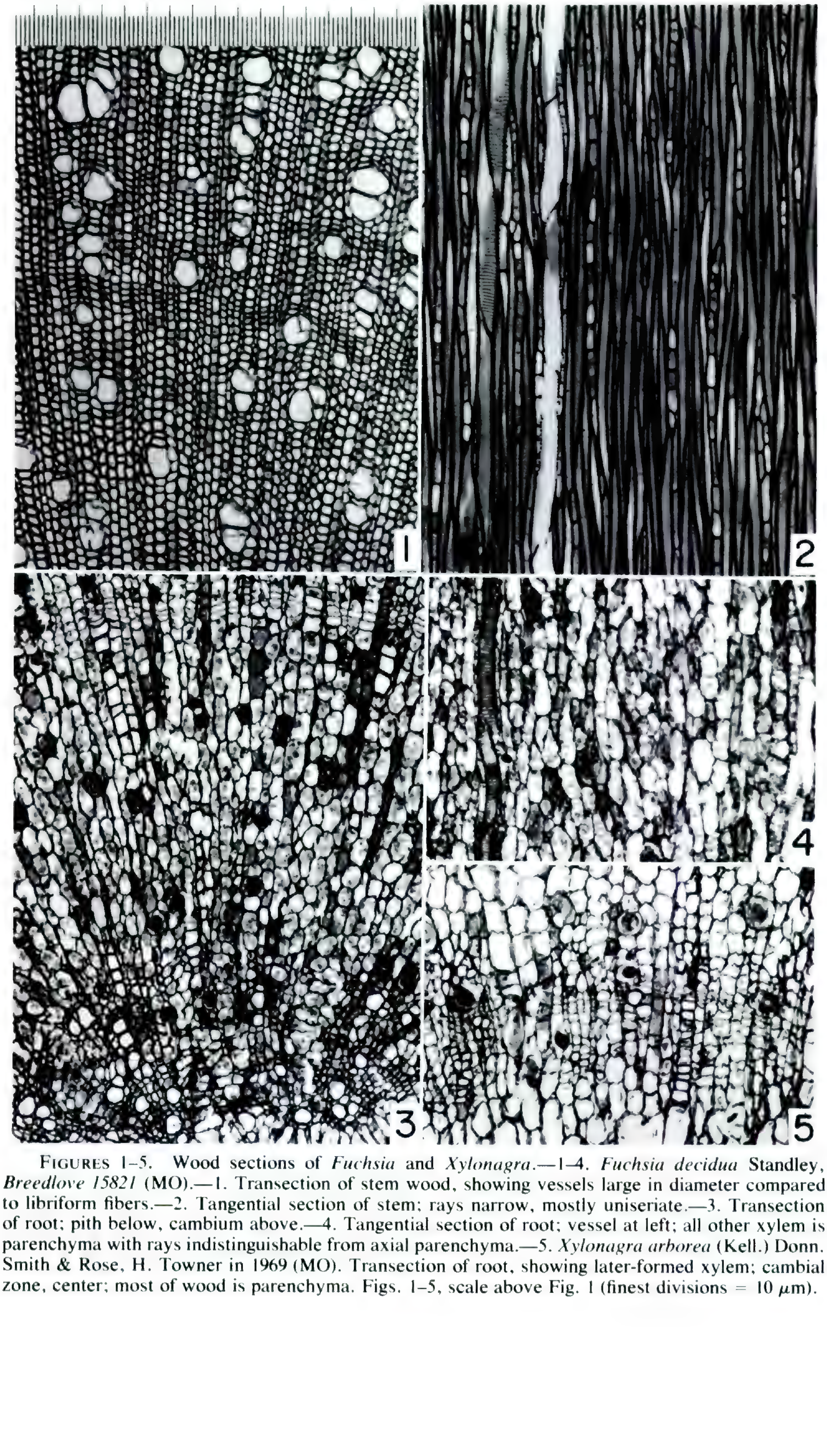
2	3	4	5	6	7	8	9	10	11	12
199/277	39/24	405	541	17	2.5	—	523	1.34	0.20/0.09	79/36
56	70	432	615	29	2.4	942	543	1.42	1.25	451
96	36	457	538	21	3.7	—	205	1.18	0.37	171
63	54	586	806	21	2.9	3478	863	1.38	0.85	500
71	52	483	747	19	3.3	1654	652	1.55	0.73	355
58	55	595	832	22	4.3	2832	1935	1.40	0.94	560
79	55	419	688	16	3.5	1896	903	1.64	0.69	291
92	51	495	791	17	3.3	3060	1235	1.61	0.56	278
130	40	491	697	19	3.5	2596	1364	1.42	0.31	151
37/61	58/37	234	316	10	2.5	210	78	1.35	1.65/0.64	386/149

Crystals.—Raphides were observed in axial parenchyma cells of *Fuchsia decidua* stems (Fig. 10). In roots of this species, cells bearing raphides occur idioblastically (Fig. 8) or in vertical pairs in the axial parenchyma that substitutes for libriform fibers. Rhomboidal crystals were observed to occur singly in ray cells of *Ludwigia bullata* and *L. peruviana*. Such crystals were reported for *Ludwigia octovalvis* (Carlquist, 1975a).

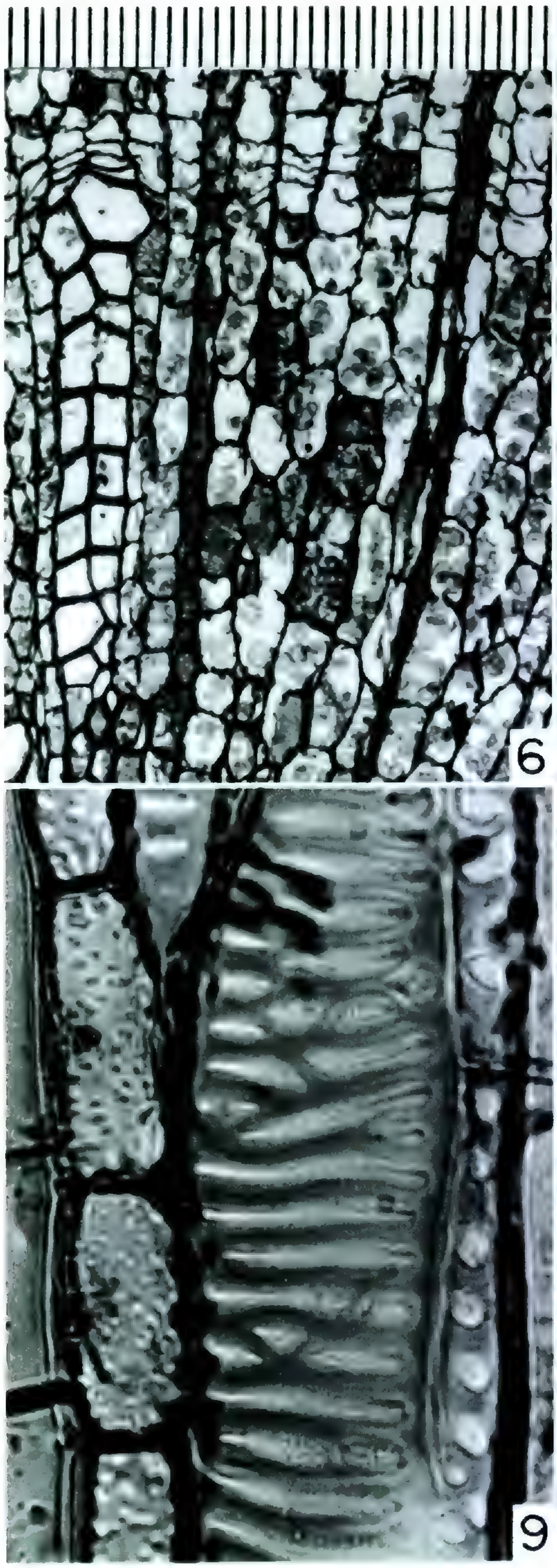
Starch; gummy deposits.—Onagraceae commonly contain starch in wood cells; starch was especially abundant in the material of *Fuchsia decidua* roots and stems (Figs. 3, 4, 6, 7, 8). Although not illustrated for stems, starch is abundant in this species in libriform fibers. Starch in libriform fibers was observed in *Lopezia suffrutescens*. In *Ludwigia elegans* and *L. peruviana*, starch was abundant in the libriform fibers, which are commonly septate. Dark-staining gummy compounds were observed in ray cells of *L. elegans*, *L. peruviana*, and *L. tomentosa*.

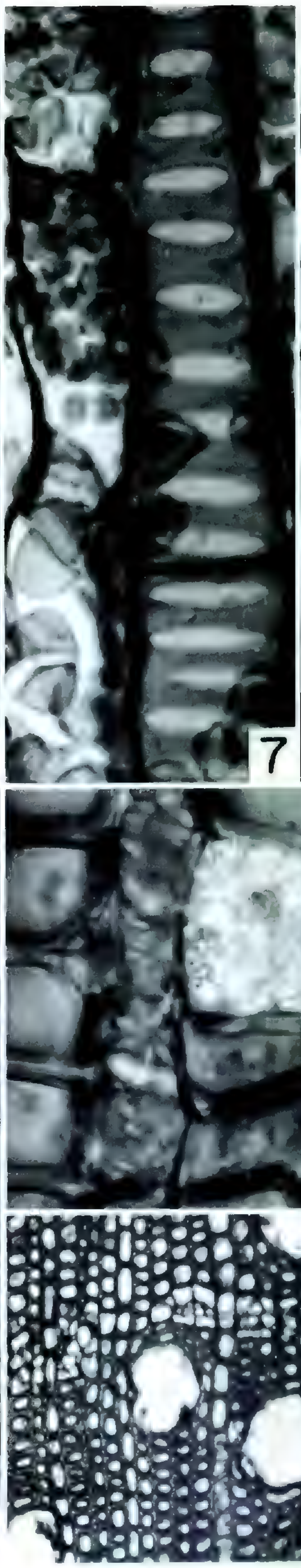
CORRELATIONS WITH HABIT AND ECOLOGY

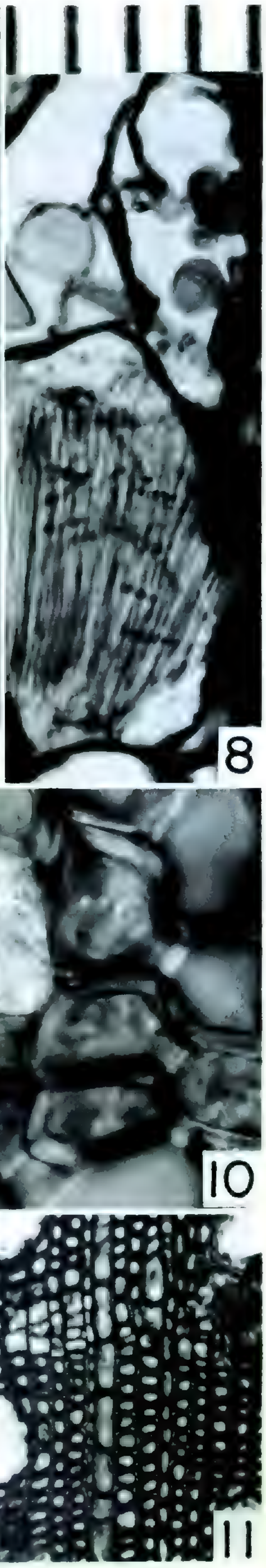
Roots.—The succulent roots of *Fuchsia decidua* and *Xylonagra arborea* show a number of interesting modifications of xylary patterns. Vessel elements are few; they are quite infrequent up to the outermost xylem in the plants studied. In the outermost xylem (Figs. 3, 5, 6) vessel elements are present. They are narrower than stem vessels (compare Figs. 1 and 3) and tend to be grouped into radial rows (Fig. 6). The vessels are angular in transectional outline, a condition that should be interpreted not in terms of primitiveness but in terms of the fact that the vessels are narrow and surrounded by cells which are few in number and wide (see Carlquist, 1975a, 1975b). The horizontal width of pits (scalariform or nearly so) and the gaping nature of pit apertures (Fig. 7) suggest that vessels are exhibiting relaxed selection for mechanical strength, in accordance with my considerations on paedomorphosis (1962, 1975b). Also persuasive of relaxed selection for mechanical strength is the substitution of parenchyma for all libriform fibers. Starch is stored abundantly in the root parenchyma of *Fuchsia decidua* and *Xylonagra arborea*; starch is also stored in the stems of *Fuchsia decidua*. The large dimensions of parenchyma cells in the roots of *Fuchsia decidua* and *Xylonagra*

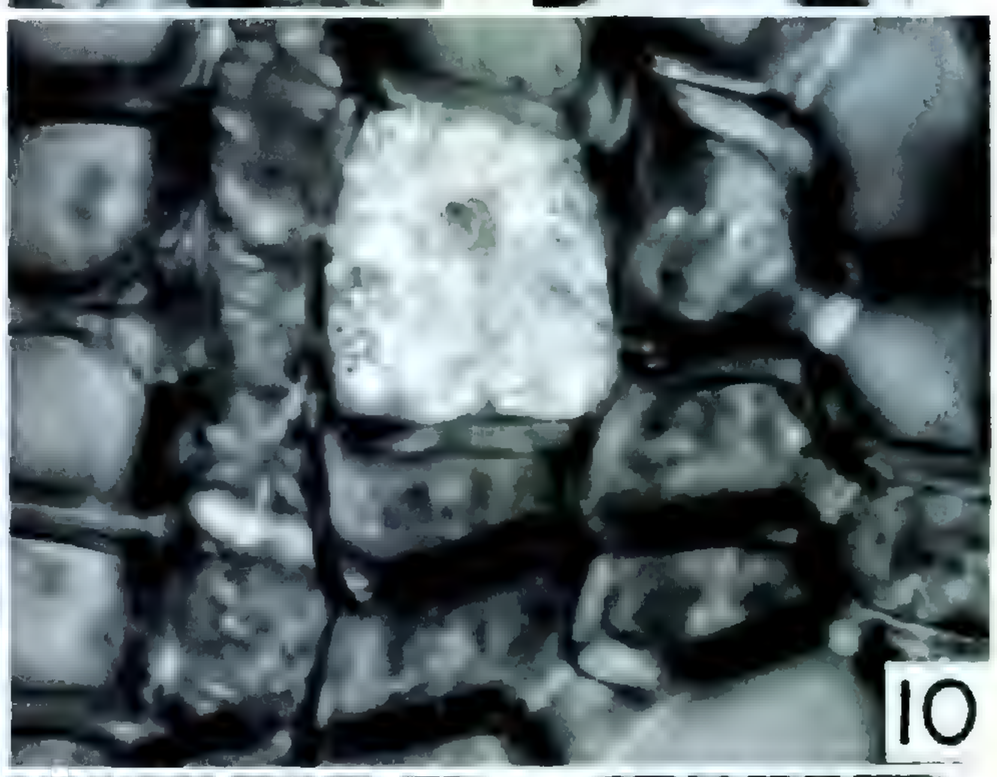


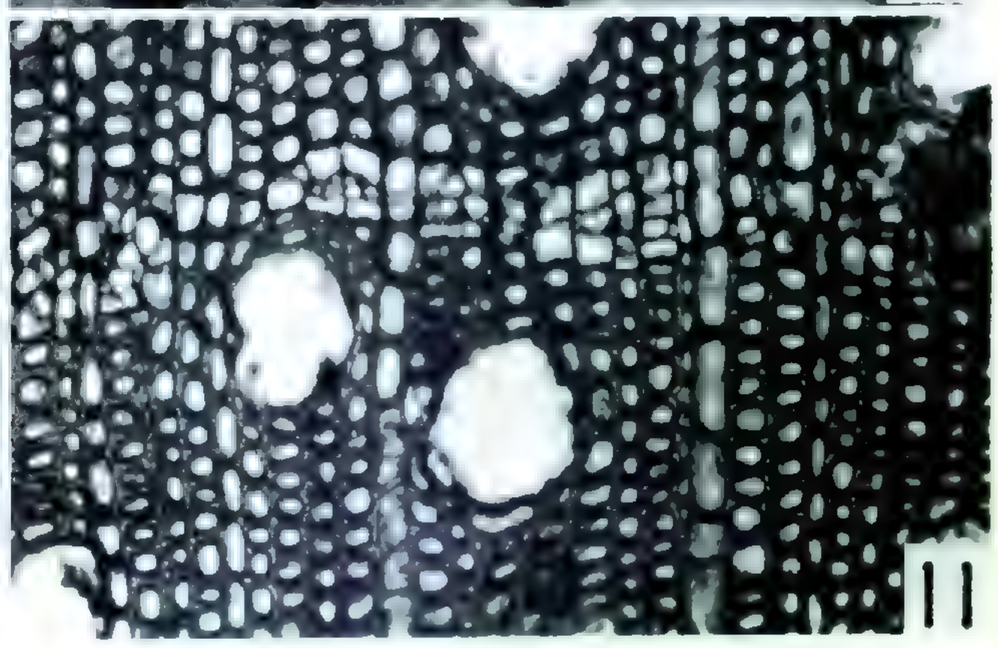
FIGURES 1–5. Wood sections of *Fuchsia* and *Xylonagra*.—1–4. *Fuchsia decidua* Standley, *Breedlove 15821* (MO).—1. Transection of stem wood, showing vessels large in diameter compared to libriform fibers.—2. Tangential section of stem; rays narrow, mostly uniseriate.—3. Transection of root; pith below, cambium above.—4. Tangential section of root; vessel at left; all other xylem is parenchyma with rays indistinguishable from axial parenchyma.—5. *Xylonagra arborea* (Kell.) Donn. Smith & Rose, H. Towner in 1969 (MO). Transection of root, showing later-formed xylem; cambial zone, center; most of wood is parenchyma. Figs. 1–5, scale above Fig. 1 (finest divisions = 10 μm).











FIGURES 6–11. Wood sections of *Fuchsia* and *Ludwigia*.—6–10. *Fuchsia decidua, Breedlove 15281* (MO).—6. Transection of root, showing radial grouping of angular vessels, left; cambial zone above.—7. Portion of tangential section of root; vessel shows vessel-parenchyma pitting; starch grains, left.—8. Portion of tangential section of root; starch grains above, raphides below.—9. Portion of tangential section of stem; vessel pitting is alternate with tendency toward scalariform.—10. Portion of transection of stem; light polarized to show raphides in axial parenchyma cell.—11. *Ludwigia sericea* (Camb.) Hara, *Ramamoorthy and Vital 642* (MO), transection of outer portion of stem wood cylinder, showing a band of interxylary phloem. Figs. 6, 11, scale above Fig. 6 (divisions = 10 μm). Figs. 7–10, scale above Fig. 8 (divisions = 10 μm).

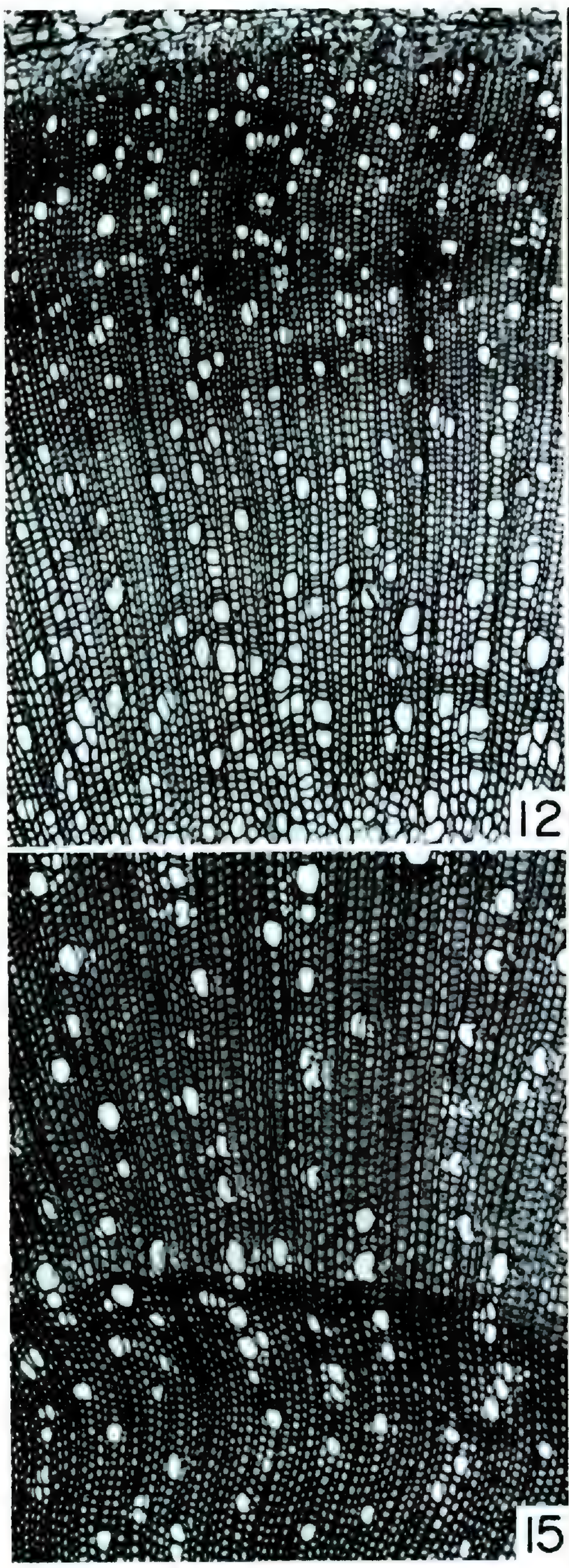
arborea seem clear indications that these roots serve for water storage also. The deciduous habit of *F. decidua* seems to confirm a water storage capability.

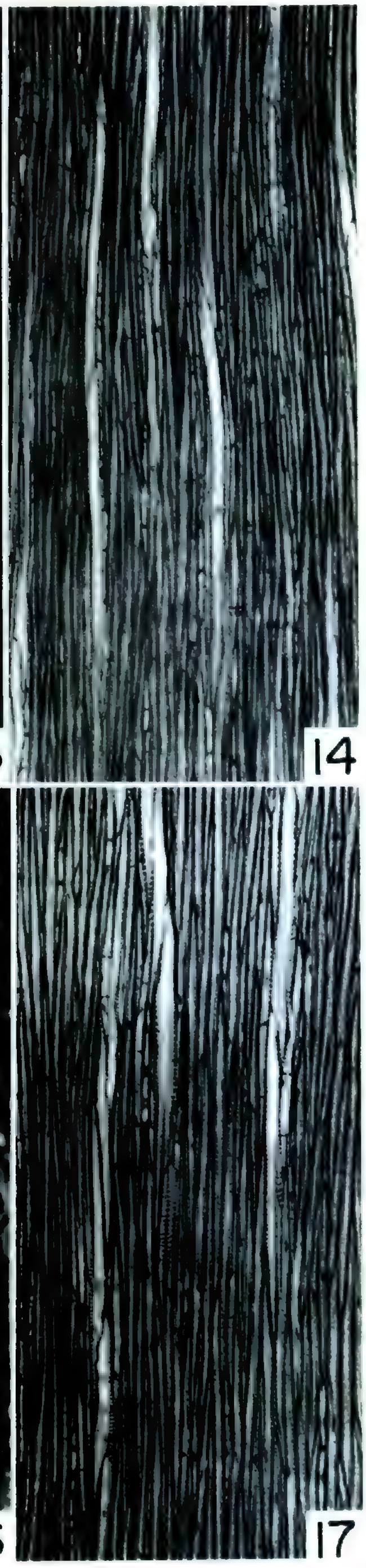
Herbaceousness.—The rather large pit apertures of vessel elements of *Lopezia suffrutescens* (Fig. 16) may relate to moderate selective pressure for mechanical strength; this species has only small stems. *Lopezia suffrutescens* also has relatively short libriform fibers. The low length ratio between libriform fibers and vessel elements in this species (1.18) is notable. In woody dicotyledons, a low ratio of this kind would indicate primitiveness; in a specialized group of herbs, it probably does not. Indeed, annual Onagraceae tend to have lower values for this ratio than trees or shrubs in the family (Carlquist, 1975a). The scalariform pattern of vessel pitting in *L. suffrutescens* (Fig. 16) may be said to be derived, in formal terms, by extension of metaxylem patterns into the secondary xylem, "paedomorphosis" (Carlquist, 1962). In functional terms, one may say that the metaxylem has low mechanical strength (there is often compensation in the form of collenchyma or, later, extraxylary fibers in the stem, or addition of libriform fibers as secondary growth commences). One may also say that secondary xylem of herbs which resembles metaxylem in vessel pitting shows relaxed selection for mechanical strength (Carlquist, 1975b).

The lack of procumbent cells in rays in most of the Onagraceae studied here could be related to herbaceousness, for subdivision of ray initials takes place over time, as pointed out by Barghoorn (1941) and stressed by numerous subsequent authors. This would account especially for the lack of square or procumbent cells in wood of *Circaea lutetiana* subsp. *canadensis*. The wood of another annual, *Oenothera deltoides* subsp. *howellii*, does have procumbent cells in rays; in this taxon, however, stems are much larger, so there is more potential opportunity for horizontal subdivision of ray initials to occur. Within the Onagraceae sampled here, rays appear to be mostly or exclusively uniseriate as secondary growth begins. This condition, however, is not necessarily related to herbaceousness at all, and may be found in a scattering of dicotyledons, such as *Illicium* (Carlquist, 1982a) and *Sarcococca* (Carlquist, 1982b).

Mesomorphy and xeromorphy.—Narrow vessels, more numerous vessels per mm^2 of transection, and short vessel elements prove to be indicators of xeromorphy (Carlquist, 1975b). These three features are apparently related to three different physiological characteristics, and therefore are not redundant; the three conjunctively are reliable as indicators, just as each alone is (Carlquist, 1982a).

Vessel diameter shows fluctuations within a stem. This is most obvious in the case of growth rings. However, wood of an annual (which might be likened to a single growth ring) also shows vessel diameter fluctuations. Vessels are wider and fewer per mm^2 at the beginning of secondary growth. This pattern is shown by both *Circaea lutetiana* subsp. *canadensis* (Fig. 12) and *Oenothera deltoides* subsp. *howellii*. Consequently, both early and late season figures have been computed for wood of these two species in Table 1. Using the vulnerability and mesomorphy indices as devised earlier (Carlquist, 1977), one can see that there is appreciably more mesomorphy at the beginning of a growth ring than at the end, assuming no change in length of vessel elements (measurements on length of vessel elements using radial sections of the two annuals showed no change in vessel element length). Certainly shift in vessel diameter and density would be





FIGURES 12–17. Wood sections of *Circaea* and *Lopezia*.—12–14. *Circaea lutetiana* L. subsp. *canadensis* (L.) Asch. & Magnus, *A. Christ in 1975*.—12. Transection; pith below, cambium above; vessel diameter decreases.—13. Vessel element from tangential section, pits alternate.—14. Tangential section, rays all uniseriate, ray cells all erect.—15–17. *Lopezia suffrutescens* Munz, *Breedlove 24534* (MO).—15. Transection; dark zone below center delimits first from second year's xylem.—16. Vessel from tangential section, showing scalariform vessel-parenchyma pitting.—17. Tangential section, showing sparse uniseriate rays. Figs. 12, 14, 15, 17, scale above Fig. 1. Figs. 13, 16, scale above Fig. 8.

ways of accommodating xeromorphy more easily than shortening of vessel element length; the latter change requires alteration of a deep-seated feature, length of the fusiform cambial initials. A number of groups show shift to wood xeromorphy by narrowing of vessels and increase in vessel density without change in vessel element length (Carlquist, 1982a, 1982b). One may say that in the case of *Circaea lutetiana* subsp. *canadensis*, the very low vulnerability ratio for end-of-season wood (0.09) is comparable to vulnerability ratios for desert plants, whereas the ratio early in the season (0.20) is only moderately xeromorphic. Shifts of this nature in the wood of an annual suggest that analysis of earlywood and latewood separately with respect to both vulnerability and mesomorphy ratios would be valuable for woody species with growth rings. Such analysis could demonstrate quantitatively precisely to what degree earlywood and latewood are mesomorphic or xeromorphic. However, even when earlywood and latewood are combined for the purposes of developing figures for vulnerability and mesomorphy in a species, comparison of species so analyzed can demonstrate how very sensitively these ratios reflect demonstrable ecological differences among species (Michener, 1981).

In species of *Ludwigia* analyzed earlier (Carlquist, 1975a), vessel elements did not seem exceptionally mesomorphic in terms of vessel diameter or density, but the length of vessel elements did seem to indicate mesomorphy for the genus as a whole. The same quantitative features are present in the six species of *Ludwigia* studied here. Paedomorphosis (Carlquist, 1962) could be used as an explanation of how relatively long vessel elements can occur in *Ludwigia*, which is a group of small to large herbs quite unlike the woody types (with relatively long vessel elements) likely to have been ancestral in the family, judging from woods of *Hauya* and *Fuchsia* (although certainly other features of those two genera are not primitive within the family).

Interxylary phloem.—In the initial study of this series (Carlquist, 1975a), distribution of interxylary phloem within Onagraceae was discussed. One criterion for presence or absence was claimed to be constituted by rapidity and seasonality of photosynthate storage and mobilization. Interxylary phloem is absent in Onagraceae with an almost continuous pattern of growth. It tends to be present in those genera and species in which growth and flowering occur suddenly and seasonally, and in which flowering and fruiting represent presumptively large energy expenditures. A second correlation cited for presence of interxylary phloem was stem size. Where stems are larger, the occurrence of one or more bands of interxylary phloem is more likely. The species in the present study lack interxylary phloem except for *Ludwigia sericea*. In the earlier study, the three species of *Ludwigia* examined lacked interxylary phloem. In *L. sericea*, stems are among the larger of the species in this genus examined; the bands of interxylary phloem occurred only near the periphery of the stem studied. These circumstances seem to validate the correlation between stem diameter and interxylary phloem. Likewise, *Lopezia suffrutescens* is informative, but in a different way. In the earlier survey, the only taxon within *Lopezia* that lacked interxylary phloem was one with relatively small stems, *L. racemosa* subsp. *racemosa*. In the present study, *L. suffrutescens* proved to lack interxylary phloem; the stems of this species are of short duration, related to the subshrub habit of this plant. However, no single

factor controls production of interxylary phloem, and in order to understand the correlations of interxylary phloem occurrence within groups where it is both present and absent, as in Onagraceae, we must take into account habit, seasonality, and massiveness of flowering and fruiting. Even then, general but not precise correlations will likely result.

Significance of Vestured Pits and Allied Structures in Dicotyledons

Vestured pits have been listed for the myrtalean families Combretaceae, Crypteroniaceae, Lythraceae, Melastomaceae, Myrtaceae, Oliniaceae, Onagraceae, Punicaceae, and Sonneratiaceae by Bailey (1933) and Metcalfe and Chalk (1950). Vestured pits also occur in the myrtalean family Penaeaceae (Carlquist & DeBuhr, 1977). Other families possessing vestured pits listed by Bailey and by Metcalfe and Chalk are Apocynaceae, Asclepiadaceae, Brassicaceae, Capparaceae, Dipterocarpaceae, Euphorbiaceae, Fabaceae, Loganiaceae, Malpighiaceae, Ochnaceae, Oleaceae, Polygonaceae, Rubiaceae, Thymeleaceae, and Vochysiaceae. Additional families in which vestured pits have been reported in recent years include Boraginaceae (Carlquist, 1970; Miller, 1977), Cistaceae (Baas and Werker, 1981), Gonystylaceae (Scurfield, Silva & Ingle, 1970), Proteaceae (Meylan & Butterfield, 1974), and Sarcolaenaceae (Baas & Werker, 1981). However, as is clear from Meylan and Butterfield (1974, 1978), the warts that comprise vestures are not restricted to the pits, but may be present both within pit cavities and also spread over walls of a vessel in such species as *Leptospermum ericoides* A. Rich., *Metrosideros robusta* A. Cunn., and *Persoonia toru* A. Cunn. This is also illustrated for two species of *Bourreria* (Boraginaceae) by Miller (1977). Also, there are examples of dicotyledon species in which warts like those in vestured pits occur on vessel walls but not within the pits themselves: *Fagus grandifolia* Ehrh., *F. orientalis* Lipsky, *F. sylvatica* L., *Platanus occidentalis* L., and *Sassafras albidum* (Nutt.) Nees. (Parham & Baird, 1974). Warted vessel walls were claimed to be part of the same phenomenon as vesturing morphologically by Coté and Day (1962), and evidence to this effect has continued to mount (Scurfield & Silva, 1970). The visual appearance of warted vessel walls and vestured pits in such species as *Leptospermum ericoides* and *Persoonia toru* (Meylan & Butterfield, 1974, 1978) is very persuasive in this regard.

If one is to include instances of warted walls, one must note that the majority of conifer woods have a warted layer (Kobayashi & Utsumi, 1951; Liese, 1951). Vessels in Gnetaceae have vestured pits (Bailey, 1933). Tracheids of Winteraceae have a warty layer much like the warty layer of conifers (Meylan & Butterfield, 1978). Warts like those on tracheid walls but too small to appear as typical vesturing occur within the pit cavities of conifer tracheids (Meylan & Butterfield, 1978).

I would like to draw attention to patterns formed by these groups. In addition, one must note that vestured pits may occur not only on vessel elements in a species, but also on tracheids in the same wood: for example, in *Alstonia* of the Apocynaceae and in *Gonystylus* of the Gonystylaceae (Scurfield, Silva & Ingle, 1970). Illustrations of this condition are offered by Meylan and Butterfield (1978)

for *Metrosideros* (Myrtaceae). One may find vesturing on vessel pits in families that lack vesturing on imperforate elements, but in many cases those imperforate tracheary elements prove to be libriform fibers (e.g., Boraginaceae, Fabaceae, Onagraceae, Rubiaceae), which can be regarded as cells not genuinely part of the "conducting system." Much remains to be learned about to what extent fiber-tracheids and tracheids in dicotyledons have vestured pits in those families where vessels have been observed to have vestured pits. However, Bailey's (1933) generalization that vestured pits relate to the conductive cells does appear to be, in general, validated as studies in electron microscopy improve our knowledge. The genera cited as exceptions to this principle by Scurfield, Silva and Ingle (1970)—*Alstonia* and *Gonystylus*—are, as noted above, genera in which tracheids, not libriform fibers, are the imperforate cell type and therefore vestured cells are still part of the conducting system rather than the mechanical system.

Warts allied in appearance to vestures have distributions that prove to be very curious and interesting. Parham and Baird (1974), on the basis of a very limited sample, thought that angiosperms with scalariform perforation plates might have warty vessel walls more frequently than angiosperms with simple perforation plates. If one reviews a larger assemblage of species (e.g., Meylan & Butterfield, 1974), one sees that this is not true. However, the correlation between wartiness of vessel walls and position of vessels within a growth ring reported by Parham and Baird (1974) is worth consideration. These authors found latewood (but not earlywood) vessels to be warted in *Fagus grandifolia*, *F. orientalis*, and *Sassafras albidum*. Ohtani and Ishida (1973) reported a similar distribution of warted walls within growth rings of *Fagus crenata* Blume.

There is a parallel to the conditions mentioned above in the tendency for helical thickenings and helical sculpture to be more prominent in latewood vessels than in earlywood vessels. Such a pattern can be seen in Asteraceae, for example. Also, one may note that in angiosperms, helical thickenings and helical sculpture occur in vessels and vascular tracheids, but not in libriform fibers (exceptions may perhaps be found, but seem not likely to bulk large). Thus, the distribution of helical thickenings is like the distribution of warted surfaces. Not all conifer tracheids have helical thickenings, but some characteristically do. A few angiosperm taxa have both helical spirals and vestured pits (e.g., *Coprosma arborea*, Meylan & Butterfield, 1978), but bulk rather small compared with the number of species that have helical sculpture but no vesturing on vessel pits. Helical sculpture has a systematic and ecological distribution which is not easy to interpret. Are forms of helical sculpture at all comparable to presence of warts on vessel walls?

We may construct a series of hypotheses for the functions of vestured pits, warts, and—if allied in nature—helical sculpture. In constructing such hypotheses, one must concede that vestured pits do not evolve in each species for which vestured pits are positively adaptive by virtue of a physiological or ecological situation. Likewise, vestured pits will not disappear immediately when a phylad evolves into an ecological condition where vestured pits are not positively adaptive—the genetic information for their formation cannot be erased immediately. If one interprets vestured pits as adaptive in Myrtales because of resistance of these structures to some factor involved in xeric conditions, evolution of some

portions of this order into moist conditions (e.g., *Fuchsia*) is not necessarily accompanied by loss of vestures, at least over short periods of geological time. Also, vascular plants have a multiplicity of devices for dealing with water relations: in some plants vessel numbers and dimensions might alter to confront ecological situations, in other plants leaf anatomy might be an effective device, while in yet others physiological pathways (crassulacean acid metabolism) or deciduousness of leaves might be invoked.

Conceding these evolutionary curricula, one may construct the following hypotheses:

1. Vestured pits can be supposed to prevent excessive deflection and rupture of pit membranes when there is a greater tension on one side of a pit membrane than on the other. This hypothesis was suggested by Zweypfenning (1978), who notes that vestured pits occur in some groups of dry situations. He seems to doubt his own hypothesis because presence or absence of vestured pits does not follow ecological conditions precisely. Although one cannot rule out Zweypfenning's hypothesis on the basis of presently available data, one must note that it does not explain instances where warts are present on vessel walls but not in pits (which are thereby vestured), nor does it explain warted borders on coniferous pits or warted inner surfaces of conifer tracheids.

2. Vestured pits and warted walls could be hypothesized to have lowered resistance to water flow. Such a hypothesis would be in line with the experiments of Jeje and Zimmermann (1979), who found that helical thickenings on vessel walls lower flow resistance as much as 40%. Such a hypothesis would subsume that all forms of relief on vessel walls would result in more rapid water flow. More importantly, such a hypothesis would assume that lessened resistance to water flow is the operative selective factor, rather than some other capability of the various forms of wall relief. Certainly simpler methods of achieving lowered resistance to water flow (e.g., wider vessels) can be envisaged. However, one may question whether the lowered resistance to water flow is the most important effect of helical sculpture presence (Carlquist, 1980). Woods rich in helical sculpture of vessels tend to occur in drier habitats (Webber, 1936; Carlquist, 1966; Michener, 1981); these species tend to have presumptively lower transpiration rates (they usually have much curtailed leaf surface) so that rapidity of flow, if that is what lowered flow resistance achieves, may not be a factor of prime selective importance. If one looks at geographical and ecological distribution of taxa in which species with and without helical sculpture occur, one sees that not only dry conditions but also frost likelihood is correlated with occurrence of helical sculpture presence (Carlquist, 1982a, 1982b). As with dry conditions, reduction of flow resistance may not be of major selective importance where frost occurs.

3. One could hypothesize that various forms of wall relief in conductive cells are mechanisms for eliminating air cavitations in vessels and tracheids and restoring normal water columns. Our ideas on how air embolisms, once formed, may be reduced are quite uncertain at the present time. I know of no data to support the idea that wall relief could function in this fashion. One could note that monocot-

yledons lack vestured pits, warted wall surfaces, and helical sculpture manifestations to a considerable degree, and that by virtue of root pressure, monocotyledons (even palms) can clear embolisms out of their vessels. While vestured pits and helical sculpture are characteristically absent from monocotyledon xylem (and from many but not all dicotyledonous vines), lack of high tensions in conductive systems may be of significance in analyzing absence of wall relief. In any case, more specific kinds of information are needed before we can consider further the idea that wall relief might be related to reduction of air cavitations in xylem.

4. One can hypothesize that vestured pits, warts, and helical sculpture increase surface area and therefore increase bonding of water molecules (hydration) to the cell surface. This, in turn, would have the effect of permitting water columns to withstand higher tensions without breaking: either the water columns in the tracheids and vessels themselves, or the portions of water columns in the pit cavities. This hypothesis would explain the presence of vestured pits (or warted pit cavities in conifers) by saying that pits represent the sites most likely to be points of entry for air bubbles under conditions of high tension. By localization of high hydration characteristics at pit cavities, the entry of air embolisms would be most effectively countered. Where relief is distributed over the entire wall (helical sculpture, grooves, warts), heightened hydration would be characteristic of an entire conducting cell, and the tension such a cell could sustain would be higher. Conducting cells with any of these forms of relief could be expected where ecological conditions of drought or physiological drought (frost, freezing of groundwater) occur. This would explain known patterns of wall relief distribution. For example, the frequency of helical sculpture is higher in species from dry areas (Webber, 1936; Carlquist, 1966) and colder areas (Carlquist, 1982a, 1982b). The warted nature of latewood as compared to non-warted earlywood in species cited earlier would also represent an interesting correlation: water tension would be higher in latewood than in earlywood.

I tend to feel that this fourth hypothesis, sketched elsewhere (Carlquist, 1982a) but elaborated here, can be supported by more numerous examples from systematic and ecological distribution of wall relief in conducting cells than can the other hypotheses at present. However, one must keep in mind that more than one tool is available to the plant in dealing with water relations. Also, any particular form of wall relief (e.g., vestured pits) must have had multiple origins if one can judge from systematic distributions. Thus, for example, in a particular locality one might find coexisting a conifer with warted tracheid walls, a legume with vestured pits in vessels, a composite with helically sculptured vessels, and a stem succulent with no relief at all on vessels. In this latter connection, one may note that forms of helical relief do happen to be infrequent, as far as we know, in stem or leaf succulents, where succulence rather than xylem anatomy is a prime tool for dealing with water relations.

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THE EVOLUTION AND SYSTEMATICS OF ONAGRACEAE: LEAF ANATOMY[1]

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ABSTRACT

Using a collection of liquid-preserved vegetative shoots representing all 17 genera of Onagraceae, I investigated the cross-sectional histology of mature leaves. The study focussed on a search for systematically useful and diagnostic features as well as on the determination of possible trends of specialization of leaf features. Exclusively dorsiventral-leaved species are found in *Ludwigia*, *Hauya*, *Fuchsia*, *Circaea*, and *Lopezia*. Leaves of these genera also have the most prominent midrib structure. The most generalized anatomy including the presence of extraxylary fibers and diverse calcium oxalate crystal structure is found in *Fuchsia*, *Ludwigia*, and *Hauya*. The other twelve genera, which belong to the tribes Epilobieae and Onagreae, show a variety of leaf specializations including xeromorphic isobilateral structure, small midribs with small midveins, the absence of extraxylary fibers, the absence of druses and styloid crystals, and a poorly differentiated mesophyll. On the basis of correlations with data from wood anatomy, pollen morphology, reproductive biology, and biogeography, I hypothesize that the Onagraceae leaves show a general reduction in leaf complexity. Leaf anatomy by itself is not diagnostic for those genera with reduced structure but it may be distinctive in the genera with more complex structure such as *Fuchsia*, *Ludwigia*, and *Hauya*.

The Onagraceae as defined by Raven (1979) comprise 674 species and 17 genera arranged in seven tribes. The family clearly belongs to the order Myrtales (Cronquist, 1968; Dahlgren, 1980; Takhtajan, 1969), but it is very distinct within the order. Onagraceae are distinguished by a distinctive four-nucleate embryo sac, the absence of alkaloids, the presence of abundant raphide crystals in vegetative tissue, and a paracrystalline-beaded pollen ektexine together with viscin threads on the pollen (Raven, 1979). Some genera have other features that are common in other Myrtalean families, including bicollateral vascular bundles, interxylary phloem, and in some cases stipules. The family may have originated in South America, where the two most primitive genera, *Ludwigia* and *Fuchsia*, center, especially in view of the clearly austral distribution of the order. The family, however, has a strong secondary center of development of the derived groups Onagreae and Epilobieae in western North America (Raven, 1979).

In addition to the fact that the leaf anatomy of the family has not been investigated thoroughly and systematically, this study was undertaken for three reasons. First, a large and comprehensive collection of liquid-preserved shoots with leaves was put at my disposal by Dr. Peter Raven. Secondly, taxonomic studies of the Onagraceae in recent years have produced a nearly complete inventory of species and a good taxonomic understanding of relationships within genera, and to some extent, between genera (review in Raven, 1979). This work has been of great value in providing accurate names for specimens being investigated anatomically, a formidable problem with most angiosperm families. The existing

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intrageneric classifications provide useful frameworks for comparing hypotheses of the evolution of leaf features. Thirdly, a number of other thorough investigations of chemistry, anatomy, and cytology of the Onagraceae have made it probably the best known flowering plant family. A sample of these include studies on wood anatomy by Carlquist (1975, 1977); on pollen by Skvarla, Raven, and Praglowski (1975, 1976) and Skvarla, Raven, Chissoe, and Sharp (1977); on flavonoids by Boufford, Raven, and Averett (1978) and Averett, Kerr, and Raven (1978). Floral anatomy has been studied by Eyde (1978, 1981, 1983) and Eyde and Morgan (1973); seeds by Seavey, Magill, and Raven (1977) and Raven, Sharp, and Keating (in prep.); reproductive biology by Raven (1979) and leaf architecture by Hickey (in prep.).

The existence of these and other previous studies is especially important. While wood anatomy, pollen morphology, and leaf architecture all have well established trends of specialization anchored in the fossil record (Dickison, 1975; Doyle & Hickey, 1976), the same cannot be said of leaf anatomy. The leaf is commonly regarded as being very variable anatomically although its variations can concur with generic, specific, or familial lines (Carlquist, 1961). Any hypothesized trends of specialization produced from this study, however, depend heavily on correlations with conclusions or data from these other studies. Among xeric-adapted species, trends of specialization are becoming better known in the light of recent comprehensive studies such as those by Pyykkö (1966) and Böcher (1979). An understanding of this type of adaptation is important in evaluating the features of leaves of some Onagraceae.

The most comprehensive comparative studies of Onagraceae leaf anatomy are those of Solereder (1908) who included 11 genera, and those of Metcalfe and Chalk (1950), who also included 11 genera but more species. Other studies that supply generally smaller quantities of data are those of Dee (1977) on *Gaura*, Carlquist and Raven (1966) on *Gongylocarpus*, Kidwal (1965) on *Fuchsia*, *Epilobium*, and *Ludwigia*, Logan and Holloway (1934) on *Fuchsia* and *Epilobium*, and Suckling (1913) on *Fuchsia*. Leaf anatomy of *Oenothera* is described by Roth (1960), Shields (1951), and Reinke (1876).

The principal questions defining the limits of this study are systematic. In general, the first consideration is whether the data from leaf anatomy correlate with the generic or tribal delimitations based upon traditional taxonomic studies. Previous literature and personal communications from other students of Onagraceae have suggested looking at a few specific problems. These include the proper tribal alignment and relationships of *Hauya*, the degree of evolutionary separation among the existing tribes, and the extent that certain features such as different types of calcium oxalate crystals define the family of tribes or genera. Special attention was paid to the tribe Onagreae, which in taxonomic schemes (Raven, 1964, 1979) seems to occupy a derived position in the family. Specifically, is the Onagreae, with its 11 genera, a natural group or a polyphyletic group of genera with certain common specialized features?

Materials and Methods

Liquid-preserved specimens representing 125 species from all 17 genera of Onagraceae were available for study. Species examined are listed following each

generic description. Specimens were collected and fixed in the field or, when marked with an asterisk, were greenhouse-grown from field-collected seed. All specimens are vouchered at MO.

Specimens for sectioning were removed from the center of each lamina and selected to produce sections of midrib and margin areas. Paraffin embedment (Johansen, 1940) was followed by sectioning at 10 μm and staining with Safranin-O and Fast Green-FCF. All descriptions were prepared from observations of leaf cross sections made perpendicular to the midribs and margins with the adaxial surface oriented uppermost in description and figure orientation. Some longitudinal and paradermal sections were made to check the orientation and dimensions of such features as extraxylary fibers and raphides. No chemical determinations were made on crystal types or on materials here called "tannins" or "gummy sheaths." Punch cards and regression analyses were used in an attempt to discern clustering or other significant patterns of feature occurrence.

OBSERVATIONS

Boisduvalia (Figs. 23–24)—The lamina is dorsiventral tending toward isobilateral and is usually thin (120–160 μm). Epidermal layers are approximately equal in thickness, smooth, and with no apparent cuticle. Stomata are common on both surfaces. Single-celled trichomes are either smooth or striate-papillate. The mesophyll is usually poorly differentiated but has one or two rows of palisade cells. Midribs are small with no distortion of the adaxial surface and a slight rounding of the abaxial surface. The midvein is a short arc with a band of abaxial phloem extending adaxially and medially around the ends of the xylem arc but not connecting in the center. Ground tissue surrounds the midveins between the epidermal layers. Laterally, the mesophyll boundary is fairly sharp and is concave, convex, or irregular. Coarse raphides found in *B. subulata* are high, low, or in mid-mesophyll, arranged horizontally and parallel to the leaf axis. Fine raphides found in other species are in thick gum sheaths, mostly horizontal in mid-mesophyll. In *B. densiflora*, the gum sheaths are dense and sclereid-like with no raphides actually seen.

Specimens examined:

B. cleistogama Curran, *Crampton 9222*, California, cult. MO. *B. densiflora* (Lindley) S. Watson, *Seavey 1095*, California, cult. MO. *B. macrantha* Heller, *Seavey 864*, California, cult. MO. *B. subulata* (Ruiz & Pavón) Raimann, *Cheese & Watson 4405* (K) Chile, cult. MO.

Calylophus (Figs. 38–40)—Leaves are isobilateral or dorsiventral (in one specimen) and variable in lamina thickness (95–400 μm). Epidermal layers are equally thick on both surfaces with no cuticle or apparent markings. Stomata are found on both surfaces except abaxial only in the dorsiventral specimen, *C. hartwegii*. The single-celled trichomes are finely tuberculate or striate-tuberculate. Very short rounded trichomes are uncommon in *C. berlandieri*. The mesophyll is usually well-differentiated with two layers of palisade cells beneath both surfaces. One layer of palisade is present in *C. hartwegii* where more than half of the mesophyll is spongy tissue. The midrib is small beneath the level adaxial surface and with only a small protrusion abaxially. The midvein is a short arc with a thin row of abaxial phloem and with a small patch of adaxial phloem seen in only one

specimen. The midvein is surrounded by ground tissue except in one specimen of *C. berlandieri,* in which ground tissue was reduced to small patches above and below the vein extending to the epidermis. In that specimen the palisade cells near the vein appeared to radiate from the vein curving toward either epidermis. In other isobilateral specimens the chlorenchyma boundary is concave, curving symmetrically around the midvein ground tissue. In *C. hartwegii,* the chlorenchyma is irregularly bounded by the midvein ground tissue. The leaf margin is rounded and normal except for the presence of a collenchymatous ridge in *C. berlandieri.* Fine raphides are common, horizontally oriented in mid-mesophyll, and unsheathed. In one specimen of *C. berlandieri,* the raphides are vertical in the palisade layers in heavy gum sheaths. In the same specimen, some are thin-sheathed and horizontal in mid-mesophyll.

Specimens examined:

C. berlandieri Spach subsp. *berlandieri, Raven 26555,* Kansas; *Rowell 16089,* Texas. *C. hartwegii* (Benth.) Raven subsp. *pubescens* (A. Gray) Towner & Raven, *Powell & Powell 2827,* Texas. *C. toumeyi* (Small) Towner, *Towner 107,* Arizona.

Camissonia (Figs. 30–32, 50–51)—The leaves are dorsiventral or isobilateral with the lamina ranging from 110 to 340 μm in thickness. Epidermal layers may be equally thick or somewhat thicker adaxially. No cuticle is distinguishable. Stomata are common on both surfaces. Trichomes are common to uncommon. Most are tuberculate, some are smooth or striate-ridged. The mesophyll is usually weakly differentiated with a palisade consisting of two cell layers or sometimes one. When spongy cells are present, the palisade occupies about half of the mesophyll. The midrib ranges from totally immersed in *C. sceptrostigma* and *C. andina* to having pronounced abaxial and adaxial ridges in *C. ovata.* The midvein is a small arc or occasionally a broad arc with a band of abaxial phloem. About half of the specimens show small patches of adaxial phloem near the margins of the xylem. Commonly, the midrib ground tissue extends between both epidermal layers with the mesophyll forming a convex boundary into the midrib. In *C. sceptrostigma* and *C. claviformis,* the palisade layer is continuous over the reduced midvein. Coarse or fine raphides may be present anywhere in the mesophyll including vertically in the palisade layer. Raphides, 40–60 μm long, are found in gum sheaths that may vary from 44 μm when resembling palisade cells to up to 300 μm long as horizontal sheaths.

Specimens examined:

C. andina (Nutt.) Raven, *R. Olds, s.n.,* 12 Jul 1976, Oregon. *C. bistorta* (Nutt. ex Torrey & A. Gray) Raven, *Knight s.n.,* s.d., California, cult., LA. *C. cheiranthifolia* (Hornem. ex Sprengel) Raven subsp. *cheiranthifolia,* cult. LA. *C. claviformis* (Torrey & Frémont) Raven, *Thompson 3816,* California. *C. lewisii* Raven, *Thompson 3747,* California. *C. ovata* (Nutt. ex Torrey & A. Gray) Raven, *Thomas s.n.,* 20 Feb 1977, California. *C. pallida* (Abrams) Raven subsp. *hallii* (Davids.) Raven, *Thomas 18473,* California. *C. sceptrostigma* (Brandegee) Raven, *Nobs 8236,* Baja California, Mexico, cult. DS, MO.

Circaea (Figs. 12–16)—The dorsiventral lamina varies in thickness from 90 to 250 μm. The adaxial epidermis is often two times as thick as the abaxial and there is apparently no cuticle. Stomata are abaxial only except in *C. cordata* where they are common on both surfaces. Trichomes are tuberculate or striate-

tuberculate. The mesophyll is usually differentiated with the one-layered palisade zone occupying one third of the mesophyll. The midrib varies from being prominent abaxially in *C. lutetiana* to totally immersed in *C. cordata*. Adaxially, the midrib may be slightly convex. Midvein xylem varies from a broad arc in *C. lutetiana* to a very small arc in *C. cordata*. Phloem forms a band abaxial to the midvein xylem in all specimens and, in the larger veins, forms two adaxial bands extending from the ends of the xylem arc that do not contact medially. The midvein is surrounded by ground tissue that is irregularly demarcated from chlorenchyma of the adjacent lamina. In *C. cordata*, the palisade layer is confluent adaxially over the midvein. Fine raphides are present, sheathed or unsheathed, mostly horizontal in mid-mesophyll.

Specimens examined:

C. alpina L. subsp. *pacifica* (Aschers. & Magnus) Raven, *Kruckeberg s.n.*, 1976, Washington. *C. cordata* Royle, *Raven s.n.*, Jul 1975, Main Botanic Garden, Moscow (seed from Vladivostok region), U.S.S.R., cult. MO. *C. erubescens* Franchet & Savat., *Sohma s.n.*, Sep 1975, Japan. *C. lutetiana* L. subsp. *quadrisulcata* (Maxim.) Aschers. & Magnus, *Raven s.n.*, Jul 1975, Main Botanic Garden, Moscow (seed from Vladivostok region), U.S.S.R., cult. MO.

Clarkia (Figs. 41–42)—Leaves are dorsiventral except isobilateral in *C. rubicunda* and *C. purpurea*. The lamina varies from 190 to 310 μm in thickness. In all dorsiventral leaves, the adaxial epidermis is always thicker than the abaxial. No cuticle is discernable. Stomata are common on both surfaces in almost all specimens. Trichomes are absent in several specimens. Where present, the trichomes are often very broad and short but sharp tipped and slightly recurved. Some trichomes are straight, long, and thin-walled. All trichomes show fine, striate-papillate or tuberculate surfaces. The mesophyll varies from well to poorly differentiated and palisade layers may be one or two cell layers thick. The midribs are generally small with slight abaxial ridges except in *C. unguiculata*, which has a prominent abaxial ridge. The mid-veins are normally a narrow arc with an abaxial band of phloem adjacent to the xylem. Only in *C. rubicunda* is any adaxial phloem seen immediately adjacent to the xylem margins. Ground tissue around the midvein is not extensive and the boundary with chlorenchyma is variable and often irregular. Fine raphides are mostly present and are found in ovate-shaped gum sheaths oriented horizontally in mid-mesophyll. In *C. rubicunda* some raphides are vertical in the palisade layer. In *C. concinna*, discrete pairs of raphide clusters often share the same gum sheath.

Specimens examined:

C. breweri (A. Gray) Greene, *Roderick 09*, California. *C. concinna* (Fischer & C. Meyer) Greene, *Roberts s.n.*, Aug 1953, California, cult. LA. *C. cylindrica* (Jepson) Lewis & Lewis, *Lewis 1433*, California, cult. LA. *C. exilis* Lewis & Vasek, *Lewis 1429*, California, cult. LA. *C. purpurea* (Curt.) Nelson & J. F. Macbr. subsp. *quadrivulnera* (Douglas) Lewis & Lewis, *MacSwain s.n.*, s.d., California, cult. UC. *C. rubicunda* (Lindley) Lewis & Lewis, s. col., California, cult. RSA. *C. unguiculata* Lindley, *Lewis 1430*, California, cult. LA.

Epilobium (except sect. *Chamaenerion*; Figs. 17, 18, 20, 22, 49)—Leaves are dorsiventral or isobilateral in most sections. *Epilobium minutum* (sect. *Crossostigma*), a spring annual, is dorsiventral. Lamina thickness ranges from 90 μm to 260 μm. Epidermal layers are approximately equally thick or either layer may be

somewhat thicker. In sect. *Cordylophorum*, the cuticle or epidermal wall is striate all over. This is also seen in *E. canum* (sect. *Zauschneria*) and in *E. oreganum* (sect. *Epilobium*). Otherwise the cuticle is not seen and the surface is smooth or sometimes striate at the margins. Stomata are common on both surfaces. Trichomes are quite variable in length and sculpturing. They may be smooth, faintly or heavily striate, tuberculate or finely papillate. The mesophyll is usually poorly differentiated with a one- or two-layered palisade. Midribs may be prominent abaxially and sometimes adaxially but more commonly are grooved or level adaxially. Midribs may be completely immersed in *E. suffruticosum*. While some midveins may be broad arcs, they are more commonly reduced to small arcs. Abaxial phloem is present adjacent to the xylem but adaxial phloem is present only in the larger midribs. Adaxial phloem is never more than small patches adjacent to the ends of the xylem arc. Tannins are very uncommon but form dense deposits in the epidermal layers of *E. consimile* and in a few cells around secondary veins of *E. hornemannii* subsp. *behringianum*. Coarse raphides are found in *E. canum*, either sheathed or unsheathed and oriented parallel to the midrib in the upper and lower mesophyll. All other species have fine raphides in gum sheaths, often horizontal in mid-mesophyll but often found in any orientation. Very long sheaths may be found in *E. coloratum*.

Specimens examined:

E. canum (Greene) Raven subsp. *canum*, *Seavey s.n.*, 1975, California, cult. MO. *E. canum* (Greene) Raven subsp. *latifolium* (Hook.) Raven, *Seavey 809*, California. *E. ciliatum* Raf. subsp. *ciliatum*, *Raven 26540*, Colorado. *E. coloratum* Biehler, Quebec, cult. MTJB 7499, cult. MO, *Raven 26289*. *E. consimile* Hausskn., *Dolgachera s.n.*, 1975, Crimea, U.S.S.R., cult. MO. *E. glabellum* Forster f., New Zealand (CHR 191388). *E. glaberrimum* Barbey subsp. *fastigiatum* (Nutt.) Hoch & Raven, *Hoch 1103*, Washington, cult. MO. *E. hornemannii* Reichenb. subsp. *behringianum* (Hausskn.) Hoch & Raven, *Dick 290*, Alaska, cult. MO. *E. komarovianum* H. Lév., New Zealand (CHR 191393). *E. leptophyllum* Raf., *Raven 26564*, Wisconsin; *Olson s.n.*, 1974, Newfoundland, cult. MO. *E. melanocaulon* Hook., New Zealand (CHR 191392). *E. minutum* Lindley ex Lehm., *Howell 51156*, California, cult. MO. *E. nevadense* Munz, *Seavey 808*, Nevada, cult. MO. *E. niveum* Brandegee, *Bowman 1192G*, California. *E. oreganum* Greene, *Seavey s.n.*, 1975, Oregon. *E. oregonense* Hausskn., *Hoch 755*, Oregon, cult. MO; *Hoch 823*, Oregon, cult. MO. *E. palustre* L., *Boufford 18795*, Ontario. *E. paniculatum* Nutt. ex Torrey & A. Gray, *Seavey s.n.*, 1975, Oregon, cult. MO. *E. pyrricolophum* Franchet & Savat., *Kubota s.n.*, 1974, Japan, cult. MO. *E. suffruticosum* Nutt., *Raven 26464*, Wyoming.

Epilobium sect. *Chamaenerion* (Figs. 19, 21)—Leaves are dorsiventral except isobilateral in *E. dodonaei* and *E. fleisheri*. The lamina ranges from 110 μm thick in *E. angustifolium* to 330 μm in *E. fleisheri*. Epidermal layers are equally thick. Cuticle or epidermal walls may be smooth or finely striate throughout. Stomata are common on both surfaces. Trichomes have narrow bases, may be nearly smooth-walled or more obviously erose-striate ridged. The mesophyll is poorly differentiated with the palisade being single-layered in dorsiventral leaves and two-layered beneath both surfaces in isobilateral specimens. The midrib is prominent abaxially and has a smaller adaxial ridge in *E. angustifolium*. In the other specimens, the midrib is largely immersed. The midvein is a broad or narrow arc of xylem with an abaxial band of phloem. Adaxial phloem is formed in two large bands extending medially from the ends of the xylem in *E. angustifolium* and *E. latifolium*. Adaxial phloem is reduced or absent in other specimens. Midrib ground tissue ranges from abundant in *E. angustifolium* to nearly absent in *E. fleisheri*.

The mesophyll boundary is irregular and often indistinct. Tannins or other granular contents are occasionally present in enlarged cells of the mid-mesophyll. Fine raphides are present, thin-sheathed or unsheathed, vertical in the palisade layer or horizontal anywhere in the mesophyll.

Specimens examined:

E. angustifolium L. subsp. *circumvagum* Mosquin, *Raven 26532*, Colorado; *Boufford 18747*, Ontario. *E. dodonaei* Villars, *Davis & Polunin 550019*, cult., Royal Botanic Garden, Edinburgh. *E. fleisheri* Hochst., s. col., France (seed from Alps), cult. MO. *E. latifolium* L. subsp. *latifolium*, *Raven 26533*, Colorado; *Hoch 1403*, Alberta.

Fuchsia (Figs. 1–3)—The lamina is dorsiventral and thin (120–180 μm). The adaxial epidermis is slightly thicker or up to twice as thick as the abaxial epidermis. No cuticle is apparent. Stomata are found exclusively on the abaxial epidermis. Trichomes are smooth-walled in most specimens but finer or coarser tuberculate surfaces are present in *F. boliviana* or *F. parviflora*. The mesophyll is well- or weakly differentiated and the palisade always consists of a single layer that occupies about one-third of the mesophyll. The midrib is very large abaxially in *F. boliviana*, *F. ravenii*, *F. lycioides*, and *F. arborescens* but smaller in other species. The midrib is totally immersed in *F. thymifolia* and *F. procumbens*. In species with larger midribs, the adaxial side also forms a small ridge. The midveins range from a well-formed semicircle in *F. boliviana* to broad arcs in most other species to a very small vein in *F. thymifolia*. Phloem forms a band abaxial to and adjacent to the xylem. In species with larger midribs the phloem also forms patches adaxial to the xylem and adjacent to it. In *F. ravenii* and *F. arborescens*, the phloem forms several series of patches within the midrib area. Species with large midribs have ground tissue surrounding the vein and extending to both epidermal layers. The ground tissue mesophyll boundary is variable and irregular. In *F. ravenii*, the mesophyll is continuous across the midrib and above the vein. Raphide crystals are occasionally coarse, mostly fine, and sheathed or unsheathed. The sheaths often appear paired. The raphides are oriented horizontally in mid-mesophyll or may be vertical in the palisade layer. Some specimens show oblique or completely random raphide orientation.

Specimens examined:

F. arborescens Sims, *Breedlove 15832*, Guerrero, Mexico, cult. UC. *F. boliviana* Carrière, cult. LA, *H. Lewis s.n.*, cult. MO. *F. encliandra* Steudel subsp. *encliandra*, *Breedlove 7178*, Oaxaca, Mexico, cult. UC. *F. lycioides* Andrews, *H. Mooney s.n.*, 1972, Chile, cult. MO. *F. microphylla* Humboldt, Bonpland & Kunth subsp. *quercetorum* Breedlove, *Breedlove 5972*, Chiapas, Mexico, cult. UC. *F. parviflora* Lindley, *Breedlove & Gregory 14251*, Durango, Mexico, cult. UC. *F. procumbens* R. Cunn., New Zealand, Tasman Botanical Garden, cult. UC. *F. ravenii* Breedlove, *Breedlove 15860*, Oaxaca, Mexico, cult. UC. *F. thymifolia* Humboldt, Bonpland & Kunth subsp. *thymifolia*, *Breedlove 15865*, Oaxaca, Mexico, cult. UC.

Gaura (Figs. 33–37)—Two-thirds of the specimens have isobilateral leaves with the remainder being dorsiventral. Thickness ranges from 130 to 290 μm. Epidermal layers are equal on isobilateral leaves and thicker adaxially on dorsiventral ones. A cuticle is generally not apparent except at the leaf margins or abaxial midribs, where it may be striate-ridged. Stomata are common on both surfaces. Trichomes are thin or thick-walled, smooth or finely papillate or strongly tuberculate. The mesophyll is well-differentiated or poorly differentiated and the

palisade tissue is always 2–3 layered. The midrib is usually prominent forming equal-sized rounded ridges on both surfaces in most isobilateral specimens. The midvein is a broad arc or a small arc in *G. biennis*. The phloem forms an abaxial band adjacent to the xylem. In all specimens except *G. biennis*, the phloem also forms a pair of adaxial bands extending medially from the ends of the xylem arc and which may or may not be directly adjacent to the xylem. The midrib ground tissue extends from the vein to both epidermal layers. In the larger isobilateral leaves with large midribs, mesophyll tissue extends into the midrib zone forming a symmetrical concave boundary against the midrib ground tissue. Leaves with smaller midribs show a less regular mesophyll boundary. Most leaves have fine raphides but coarse raphides occur in *G. suffulta* and *G. angustifolia*. Raphides may be with or without gum sheaths. They are horizontal in mid-mesophyll or often vertical in the adaxial or abaxial palisade. The heavy gum sheaths may resemble sclereids in *G. lindheimeri*, *G. demareei*, and *G. longiflora*. Druses were seen in a specimen of *G. angustifolia*. *Gaura longiflora*, *G. demareei*, and *G. biennis* are very closely similar species of sect. *Gaura*, *G. angustifolia* and *G. lindheimeri* are less closely similar species of the same section.

Specimens examined:

G. angustifolia Michaux, *Boufford 18409*, Florida. *G. biennis* L., *Sorensen 5111*, Iowa, cult. MO. *G. demareei* Raven & Gregory, *Hoff s.n.*, 1976, Texas. *G. lindheimeri* Engelm. & A. Gray, s. col., Texas, cult. UC. *G. longiflora* Spach, *Boufford & Lorence 18864*, Missouri. *G. mutabilis* Cav., *Rzedowski 29135*, Mexico, cult. MO. *G. parviflora* Douglas, *Hoff s.n.*, 1976, Texas. *G. suffulta* Engelm. ex A. Gray subsp. *suffulta*, *Benbow 75*, Texas. *G. villosa* Torrey subsp. *villosa*, *Raven 26552*, Kansas.

Gayophytum (Fig. 29)—The leaves are isobilateral but have better developed palisade tissue on the adaxial side. The lamina is ca. 210 μm thick. Epidermal layers are of equal thickness and have no apparent cuticle. Stomata are common on both surfaces. Trichomes were not seen. The mesophyll is not well differentiated but there is a two layered adaxial palisade and one abaxial palisade. The midrib is slightly convex abaxially and slightly grooved adaxially. The midvein is a broad arc with an abaxial band of phloem adjacent to the xylem and two well-developed bands of phloem adaxially. They extend medially from the ends of the xylem but do not connect and are separated from the xylem by ground tissue. Ground tissue extends to the epidermal layers above and below the midvein but laterally the midvein ends are within the mesophyll. Fine raphides (to 60 μm long) in their gum sheaths are vertical in the adaxial palisade or horizontal in mid-mesophyll. Some laticifer-like long gum sheaths may extend to 250 μm.

Specimen examined:

G. heterozygum Lewis & Szweyk., *Chambers 4227*, Oregon.

Gongylocarpus (Figs. 25, 26)—The dorsiventral lamina varies in thickness from 130 to 250 μm. The adaxial epidermis is slightly thicker or up to double the thickness of the abaxial epidermis. Epidermal surfaces are smooth or slightly striate. Trichomes are absent or uncommon adaxially over the midrib. The single-celled trichomes have a thin, minutely tuberculate wall. Stomata have guard cell pairs of equal length and width (ca. 24–28 μm) and are common on both surfaces.

The adaxial surface is level over the midrib while the abaxial surface has a slight rounded protrusion. Midrib vasculature is a small flattened arc with 4–5 patches of abaxial phloem. Midvein ground tissue surrounds the vein and is demarcated from chlorenchyma by an irregular vertical boundary. In a smaller leaf the midvein is embedded in chlorenchyma except for a small abaxial patch of ground tissue. The well-differentiated chlorenchyma has a palisade layer slightly thinner than the spongy layer. Columnar palisade cells are well-formed or somewhat irregular. One layer of angular collenchyma may be present beneath both midrib epidermal layers. Raphide crystals, mostly in gum sheaths, are common and are either coarse or fine. Some bundles of prismatic crystals (8 × 40 μm) may also be present. Crystal sheaths are up to 60 μm long and are horizontally oriented in mid-mesophyll.

Specimen examined:

G. rubricaulis Schlecht. & Cham., *Breedlove 41880*, Chiapas, Mexico, cult. MO.

Hauya (Figs. 7, 8)—The dorsiventral lamina is about 130 μm thick and the adaxial epidermis is slightly thicker than the abaxial. Epidermal layers are smooth but cuticle ridges are visible in the boundary depressions between epidermal cells. Stomata are restricted to the abaxial epidermis with guard cell pairs about 20 μm long and 16 μm wide. Trichomes have birefringent walls and are common on adaxial and abaxial surfaces of veins. They are often coarsely tuberculate. The mesophyll is well differentiated consisting of one palisade layer occupying one-third of the mesophyll. The midrib is very prominent abaxially with only a slight ridge adaxially. The midvein is a large, well developed, semicircle open adaxially. A prominent band of abaxial phloem is present and numerous adaxial patches of phloem are found in the ground tissue within the xylem semicircle. Outside of the abaxial phloem is a layer of extraxylary fibers. The secondary veins have adaxial fiber extensions. The midrib ground tissue is well-demarcated from the mesophyll with an irregularly shaped boundary. Tannins are present in the phloem region of the midrib and in about six abaxial layers of midrib ground tissue. Styloid crystals with pointed or blunt ends are common and variously oriented in mid-mesophyll and around veins. Druses are less commonly found and loosely clustered. They also occur around veins. Fine raphides in long gum sheaths (to 65 νm) may also be common near veins.

Specimens examined:

H. elegans DC. subsp. *cornuta* (Hemsl.) Raven & Breedlove, *Raven and Breedlove s.n.*, s.d., Chiapas, Mexico, cult. UC. *H. heydeana* Donn. Sm., *Breedlove 42080*, Chiapas, Mexico, cult. MO.

Heterogaura (Fig. 43)—Leaves are dorsiventral with a lamina thickness of 160 μm. The epidermal layers are equal in thickness and have no apparent cuticle. Stomata are common on both surfaces. Trichomes have thin, smooth walls and are uncommon. The mesophyll is not well-differentiated with the single palisade layer occupying about 40% of the mesophyll. The midrib is slightly ridged abaxially and has a small adaxial groove. The midvein is a small arc of xylem with a band of abaxial phloem. Small patches of adaxial phloem occur near the margins of the xylem. The midrib is surrounded by a small zone of ground tissue that

extends to the abaxial epidermis. It may extend to the adaxial epidermis or the palisade cells may be continuous over the vein. Commonly, the chlorenchyma is concave in its boundary with the ground tissue. Fine raphides in gum sheaths may be vertically oriented in the palisade tissue or may be horizontal in mid-mesophyll.

Specimen examined:

H. heterandra (Torrey) Cov., *Lewis 1628*, California.

Lopezia (Figs. 9–11, 48)—The leaves are dorsiventral with the lamina thin to thick (120–370 μm). Epidermal layers are mostly equal in thickness or slightly thicker adaxially. Adaxial epidermal cells may be uniformly or occasionally markedly convex in some species. No cuticle is apparent. Stomata are mostly abaxial only although a few specimens had adaxial stomata. Trichomes are absent or not seen in most specimens. The adaxial epidermal cells are papillate in *L. miniata*. When present, trichomes are sclerotic and smooth-walled. The mesophyll is usually well-differentiated and the one-layered palisade occupies approximately 30–50% of the mesophyll. The midrib usually is large, forming a prominent ridge abaxially while the adaxial surface is nearly level. The midvein is a large semicircle in *L. grandiflora* and *L. langmaniae*, a broad arc in most other species or a small arc in *L. nuevo-leonis*. Phloem forms an abaxial band adjacent to the xylem, and in the larger midveins, some adaxial phloem is usually formed as individual patches or rows, not necessarily adjacent to the xylem. Midrib ground tissue surrounds the vein between the epidermal layers in the large midribs. The boundary with adjacent mesophyll is variable and irregular. In *L. ovata*, *L. gentryi*, and *L. nuevo-leonis*, the palisade is continuous adaxially to the midvein. In *L. langmaniae*, the adaxial phloem contains gum ducts oriented parallel to the vein. Fine raphides are present in all specimens and quite variable. They may be with or without gum sheaths and they may be horizontal in mid-mesophyll or vertical in the palisade layer. The raphides may be replaced entirely leaving "sheaths" resembling sclereids (*L. racemosa*, *L. miniata*, *L. nuevo-leonis*, *L. grandiflora*). Some sheaths are elongate resembling ducts.

Specimens examined:

L. concinna Raven, *Reveal and Hardy 4064*, Sinaloa, Mexico, cult. MO. *L. gentryi* (Munz) Plitmann, Raven & Breedlove, *Breedlove 15551*, Durango, Mexico, cult. MO. *L. grandiflora* Zucc. subsp. *grandiflora*, *Breedlove 39154*, Oaxaca, Mexico, cult. MO. *L. grandiflora* Zucc. subsp. *macrophylla* (Benth.) Plitmann, Raven & Breedlove, *Breedlove 22704*, Chiapas, Mexico. *L. langmaniae* Miranda, *Breedlove 7161*, Chiapas, Mexico, cult. MO. *L. longiflora* Decaisne, *Breedlove 8044*, Morelos, Mexico, cult. MO. *L. miniata* Lag. ex DC. subsp. *miniata*, *Boutin & Brandt 2165*, Jalisco, Mexico; *Carlquist s.n.*, Mexico, cult. Stanford, *Raven 66-22*. *L. nuevo-leonis* Plitmann, Raven & Breedlove, *Ripley & Barneby 13569*, Nuevo León, Mexico, cult. MO. *L. ovata* (Plitmann, Raven & Breedlove) Plitmann, Raven & Breedlove, *Breedlove 4255*, Durango, Mexico, cult. Stanford. *L. racemosa* Cav. subsp. *racemosa*, *Thompson 3797*, Mexico, cult. LA. *L. racemosa* Cav. subsp. *moelchenensis* Plitmann, Raven & Breedlove, *Breedlove 7794*, Chiapas, Mexico, cult. Jerusalem, *Plitmann 68-2*. *L. riesenbachia* Plitmann, Raven & Breedlove, *Anderson & Anderson 5626*, Oaxaca, Mexico, cult. MO. *L. semeiandra* Plitmann, Raven & Breedlove, *Breedlove 19163*, Sinaloa, Mexico, cult. MO. *L. suffrutescens* Munz, *Breedlove 24534*, Durango, Mexico, cult. MO.

Ludwigia (Figs. 4–6)—The leaves are always dorsiventral with the lamina thickness ranging from 60 to 190 μm. Thickness of epidermal layers is equal on

both surfaces. No cuticle is evident and epidermal surfaces are usually smooth. Striate ridges may be present abaxially on veins and at the margins in *L. peruviana* and *L. suffruticosa*. Stomata are equally common on both surfaces. Trichomes may be absent but when present are commonly single-celled. Walls are usually thin and smooth but they may be finely papillate or striate-papillate. Trichomes of *L. peruviana* are often 2-celled or up to 5–6 cells, unbranched. The mesophyll is well-differentiated with one adaxial layer of palisade occupying about half of the mesophyll. The midrib of the more generalized species is very prominent and rounded abaxially. There is also a high, flattened, adaxial ridge above the midrib. The midveins in these species are well-formed semicircles with an abaxial layer of phloem. Adaxially, the phloem forms small patches randomly in the ground tissue within the xylem semicircle. Species with this type of midrib-midvein anatomy include *L. erecta L. lagunae*, *L. leptocarpa*, *L. maritima*, *L. peploides*, *L. peruviana*, *L. pilosa*, *L. polycarpa*, and *L. suffruticosa*. Other specimens studied show little or no adaxial ridge, less prominent rounding abaxially, a midvein consisting of a broad or smaller arc, loss of the adaxial phloem, and, in the smallest leaves, a continuous palisade layer across the adaxial side of the midrib. This more specialized type of leaf structure is found exclusively in some of the more advanced sections, such as sect. *Dantia*, but is scattered through the other groups as well. Patches of perivascular fibers are found abaxial to the midvein in *L. peruviana* and *L. suffruticosa*. The midrib ground tissue usually surrounds the midvein, and the boundary with the adjacent mesophyll is variously shaped. In the largest veins (*L. peruviana*) the palisade tissue curves upward into the adaxial ridge. Thick-walled secretory idioblasts are present just beneath both epidermal layers in *L. sedoides*, a floating aquatic plant. Calcium oxalate crystals are present in all samples of *Ludwigia*. Fine raphides are present in nearly all specimens and coarse raphides in five. Raphides are unsheathed and usually horizontal in mid-mesophyll. Druses are also present in a majority of specimens and appear as loosely aggregated groups of prismatics. They are present in mid-mesophyll and in the midvein phloem region. In *L. palustris* styloids or coarse raphides are found oriented vertically in the mesophyll.

Specimens examined:

L. alata Elliott, *Arguelles 3*, Mississippi. *L. arcuata* Walter, *Hilsenbeck 668* (USF), Florida. *L. caparosa* (Cambess.) Hara, *Ramamoorthy & Jones 118*, Brazil. *L. decurrens* Walter, *Raven 26469*, Arkansas. *L. densiflora* (Micheli) Ramamoorthy, *Ramamoorthy 650*, Amazonas, Brazil. *L. erecta* (L.) Hara, *Hatschbach s.n.*, 1976, Brazil. *L. lagunae* (Morong) Hara var. *paraguayensis* (Chodat) Munz, *Ramamoorthy 1019*, Paraguay, cult. MO. *L. leptocarpa* (Nutt.) Hara, *Raven 26491*, Arkansas. *L. linearis* Walter, *Boufford & Wood 18899*, North Carolina. *L. longifolia* (DC.) Hara, *Ramamoorthy & Jones 115*, Brazil. *L. maritima* Harper, *Hilsenbeck 669* (USF), Florida. *L. microcarpa* Michaux, *Boufford 18047*, Florida; *Hilsenbeck 667* (USF), Florida. *L. myrtifolia* (Cambess.) Hara, *Ramamoorthy et al. 81*, Brazil. *L. nervosa* (Poir.) Hara, *Hatschbach s.n.*, 30 Jan 1976, Brazil. *L. palustris* (L.) Elliott, *Boufford 18562*, Florida; *Willingham 598*, Georgia; *Arguelles 2*, Mississippi. *L. peploides* (Humboldt, Bonpland & Kunth) Raven subsp. *glabrescens* (O. Kuntze) Raven, *Raven 26493*, Arkansas. *L. peruviana* L., *Anderson 4082* (FSU), Florida. *L. pilosa* Walter, *Boufford 18496*, Florida. *L. polycarpa* Short & Peter, *Raven 26523*, Missouri. *L. sedoides* (Humboldt, Bonpland & Kunth) Hara, *Croat 38286*, Panama. *L. sericea* (Cambess.) Hara, *Ramamoorthy et al. 68*, Brazil. *L. spathulata* Torrey & Gray, *Boufford 18564*, Florida. *L. suffruticosa* Walter, *Hilsenbeck 670* (USF), Florida. *L. virgata* Michaux, *Willingham 597*, Georgia.

Oenothera (Figs. 46, 47)—Specimens are about evenly divided among dorsiventral and isobilateral anatomy. Laminas are very thin (120 μm) ranging to very

thick (490 μm). Epidermal layers are equally thick or much thicker adaxially. No cuticle is apparent except at the margins where, in some specimens, sharp ridges are formed. Stomata are equally common on both surfaces. Trichomes were not seen in a third of the specimens. When present, trichomes are smooth-walled, striate-ridged, papillate, tuberculate, or echinate. They may be thin-walled or heavy-walled and lignified. The mesophyll is either well- or poorly differentiated and has a palisade consisting of two layers except for one layer in *O. scabra*. Midrib shape is quite variable. In larger leaves the midrib has an abaxially prominent ridge. The ridge may be equally prominent adaxially as in *O. macrosceles* and *O. centauriifolia* or broadly grooved adaxially as in *O. grandiflora* and *O. grandis*. In smaller-leaved species, midribs are immersed as in *O. mendocinensis*, *O. scabra*, and *O. hookeri*. Midveins are broad arcs or narrow arcs. Phloem forms an abaxial band adjacent to the xylem. In leaves with large midribs and broad xylem arcs, single adaxial bands of phloem extend medially from the ends of the xylem and not immediately adjacent to the xylem adaxially. The midvein is generally surrounded by ground tissue extending to both epidermal surfaces except in the small midribs. The lateral boundary with the mesophyll is variable but predictable in the different shaped midribs. Margins may have a ridge of lignified and collenchymatous cells in *O. macrosceles*. Almost styloid-like coarse raphides occur in *O. macrosceles* and in a few other species. Most specimens contain fine raphides also or exclusively. They occur with or without gum sheaths, horizontal in mid-mesophyll, or vertically in the adaxial palisade. In some specimens heavy gum sheaths occur giving a sclereid-like appearance.

Specimens examined:

O. caespitosa Nutt. subsp. *macroglottis* (Rydb.) Wagner, Stockhouse & Klein, *Raven 26536*, Colorado. *O. centauriifolia* (Spach) Steudel, s. col., Uruguay, cult. MO. *O. elata* De Vries, *Stubbe s.n.*, 1969, California. *O. grandiflora* L'Hér. ex Ait., *Steiner 1952*, Mississippi. *O. grandis* (Britton) Smyth, *Benbow 81*, Texas. *O. macrocarpa* Nutt. subsp. *macrocarpa*, *Boufford & Lorence 18868*, Missouri. *O. macrosceles* A. Gray, *Gentry 14568*, Venezuela, cult. MO. *O. mendocinensis* Gillies ex Hooker & Arnott, *Santarius 421*, Argentina, cult. Düsseldorf. *O. parviflora* L., *Boufford 18741*, Ontario. *O. ravenii* Dietrich subsp. *argentinae* Dietrich, *Hecht 31*, Uruguay, cult. Düsseldorf. *O. rhombipetala* Nutt. ex Torrey & Gray, *Benbow 82*, Texas. *O. scabra* Krause, *Diers s.n.*, 1959, Argentina, cult. Düsseldorf. *O. spachiana* Torrey & Gray, *Straley 751*, Louisiana.

Stenosiphon (Figs. 44, 45)—The lamina is isobilateral and thick (310–380 μm). The epidermal layers are equally thick on both surfaces (20–25 μm) and covered with a smooth, well-developed cuticle. Trichomes were not seen. Stomata are common on both surfaces. The mesophyll is composed of well-formed columnar palisade cells, two layers beneath adaxial and abaxial epidermal layers. The midrib is large and protrudes as a rounded ridge symmetrically on either surface. The midvein is a broad arc with well-developed abaxial patches of phloem. Two adaxial bands of phloem adjacent to each edge of the xylem do not connect at the center. They are separated by ground tissue from the xylem. Midrib ground tissue surrounds the midvein. In the largest specimen, the chlorenchyma has a concave pattern at the midrib, is sharply demarcated from the ground tissue, and is symmetrically disposed laterally and dorsiventrally. In another specimen, the chlorenchyma is less sharply demarcated and has irregular vertical boundaries. The lamina has a well-defined ridge of thick-walled cells extending beyond the mesophyll. Tannins fill the cells in secondary vein sheaths, epidermal cells, and rows

of cells around the midvein. Coarse or fine raphides occur mostly in heavy red sheaths that are vertical in either palisade layer. Some fine raphides may occur horizontally without sheaths in mid-mesophyll.

Specimens examined:

S. linifolius (Nutt.) Heynh. *Raven 26563*, Kansas; *Benbow 83*, Texas.

Xylonagra (Figs. 27, 28)—The lamina of these dorsiventral leaves ranges from 130 to 170 μm in thickness. Epidermal layers are approximately equally thick and have no apparent cuticle. Stomata are common on both surfaces. Trichomes are uncommon and have boldly tuberculate walls. Mesophyll differentiation is poor with the single palisade layer occupying 40–50% of the mesophyll. The midrib forms a pronounced abaxial ridge and has a tendency toward a smaller adaxial ridge. The midvein varies from a broad arc to a very small arc. Phloem is mostly in an abaxial band with some adaxial phloem patches near the margins of the xylem arc. Midrib ground tissue surrounds the vein between epidermal layers. The mesophyll boundary is well marked and is convex laterally into the midrib ground tissue. Raphides are fine, mostly without gum sheaths, and are horizontal in the mid- or upper mesophyll.

Specimens examined:

X. arborea (Kellogg) Donn. Sm. & Rose, *D. Verity s.n.*, s. d., Baja California, Mexico, cult. LA and MO.

DISCUSSION

DISTRIBUTION OF ANATOMICAL FEATURES (see Table 1)

Leaves of Onagraceae are usually ovate, elliptical or linear with margins mostly entire or possessing small irregular teeth. They may be long- or short-petiolate and hydric to xeromorphic in structure. The leaves are exclusively dorsiventral in eight genera, exclusively isobilateral in only *Stenosiphon*, and with both conditions present in different species of seven genera. Five of the exclusively dorsiventral genera constitute entire tribes: *Circaea*, *Fuchsia*, *Hauya*, *Lopezia*, and *Ludwigia*. The other three, *Gongylocarpus*, *Heterogaura*, and *Xylonagra*, are placed in the Onagreae with seven other genera that have both dorsiventral and isobilateral leaves, as do the two genera of the remaining tribe, Epilobieae. It seems clear from this distribution that dorsiventral leaves are primitive in the family, and that isobilateral leaves have evolved on a number of occasions in the advanced tribes Onagreae and Epilobieae.

Midribs with the most prominent structure occur in leaves of the exclusively dorsiventral genera. As seen in transection, a marked abaxial protrusion may exceed an arc of 230° and contain a prominent semicircular midvein in species of *Ludwigia*, *Fuchsia*, *Lopezia*, and *Hauya*. This seems clearly to be the primitive condition for the family. In addition, a prominent adaxial ridge is common over the midrib in species of *Ludwigia*, *Fuchsia*, and *Gaura*. The majority of species of Onagraceae have midribs that are level with the mesophyll adaxially and that protrude abaxially in an arc varying from 90° to 180°. These midribs contain midveins that are either short or broad arcs. All isobilateral leaves have these

less curved midveins. The most highly developed isobilateral leaves have midribs that protrude adaxially and abaxially to the same degree. These include *Epilobium oreganum, Gaura angustifolia, G. demareei, G. parviflora, Oenothera centauriifolia, O. macrosceles,* and *Stenosiphon linifolius*.

Leaf margins between teeth are normally rounded in transection and contain no unusual histology. In a few strongly isobilateral species (*Calylophus berlandieri, Oenothera macrosceles, Stenosiphon linifolius*) the margin is comprised of a ridge of thickened cells. This zone, three to eight cells in from the margin, is collenchymatous or, in *O. macrosceles,* partially lignified. The margin zone is distinctly demarcated from the mesophyll and appears to provide strong mechanical protection.

Leaf teeth, apparently best formed in the genus *Fuchsia,* show an unusual hydathodal structure that Hickey (1981) has called the Fuchsioid tooth. It appears to have the same structure as the Rosoid tooth described by Hickey and Wolfe (1975). This structure has a subepidermal foramen or space that opens to the outside through one or more stomata. Beneath the foramen is a zone of elongated secretory cells that connect to a vein ending well within the margin (Figs. 48–51). The vein, appearing to be a single structure in transection, is seen in cleared leaves to be formed of a strong median vein flanked by two smaller veins that converge and fuse just beneath the area of secretory cells (Hickey, this symposium). The Fuchsioid tooth has been found among other families of Myrtales only in Lythraceae (L. Hickey, pers. comm.). It can be seen clearly in *Ludwigia, Lopezia, Fuchsia, Camissonia, Gaura,* and *Epilobium,* and is probably present in most other genera, even those with very reduced teeth. DeCastells et al. (1979) describe and illustrate this structure in five species of *Ludwigia*. Studies on the woody Saxifragaceae by Stern (1974, 1978) and Styer and Stern (1979a, 1979b) record the presence of a very similar type of hydathodal tooth.

The adaxial epidermal cells are up to twice as thick as the abaxial epidermal cells on dorsiventral leaves. The two layers are identical on many dorsiventral-leaved species and on all isobilateral leaves. Epidermal cells are most commonly horizontally elongate and convex on the outer surface but true papillate cells were recorded in *Lopezia miniata*. In other *Lopezia* species, epidermal cells are commonly of two sizes, conspicuously high and convex cells are interspersed with low flat cells. Midrib epidermal cells in *Hauya* are high and narrow in transection and elongate parallel to the midrib.

Little apparent difference in this study was noted between greenhouse-grown and field-grown plants regarding cuticle thickness. However this feature should be interpreted cautiously because Hull, Morton and Wharrie (1975) showed that cuticular development is normally much greater on outdoor grown plants. The cuticle layer is very thin in most specimens. It is generally thicker at the margins and above and below the midrib. The thicker marginal cuticle is usually longitudinally striate with striations being especially prominent in *Boisduvalia subulata, Calyophus berlandieri, Epilobium angustifolium, E. leptophyllum, E. oreganum, Gaura lindheimeri, G. parviflora, G. suffulta, G. villosa,* and *Oenothera macrosceles*. In *Hauya elegans,* the cuticle is flanged and conspicuously thickened in the grooves between epidermal cells.

Stomata are evenly dispersed over both epidermal layers in all genera except

TABLE 1. Leaf characters of Onagraceae.* (Continued on facing page.)

	Dorsiventral	Isobilateral	Midrib Protrudes Adaxially	Midrib Protrudes Abaxially	Midvein Semicircle	Midvein Broad Arc	Midvein Short Arc	Midvein with Adaxial Phloem	Abaxial Periphloic Fibers	Palisade Layers**	Mesophyll Well-differentiated	Mesophyll Poorly-differen.	Epidermal Thickness: Adaxial = Abaxial	Epidermal Thickness: Adaxial > Abaxial
Ludwigia	+		+	+	+	+	a	+	a	1	+	a	+	a
Hauya	+			+	+			+	+	1	+			+
Lopezia	+		±	+	+	a	+	+		1(2)	+	+	+	+
Fuchsia	+			+	+	+	+	+	+	1	+	+	a	+
Circaea	+			+		+	+	+		1		+		+
Epilobium	+	+		+	a	+	+	+		1–2	+	+	+	a
Boisduvalia	+	+		+			+	+		1–2	±	+	+	
Gongylocarpus	+			+			+	+		1	+			+
Gaura	+	+	+	+		+	±	+		2–3	+	+	+	
Camissonia	+	+	a	+		+	a	+		1–3	±	+	+	±
Gayophytum		+				+		+		2		+		+
Xylonagra	+		±	+			+	+		1		+		+
Calylophus	+	+		+			+	+		1–3	+	a	+	
Clarkia	+	a		+			+	+		1–2	+	a	+	±
Heterogaura	+			+			+	+		1		+	+	
Oenothera	+	+	+	+		+	+	+		1–2	+	+	+	+
Stenospiphon		+	+	+		+		+		2	+		+	

* Symbols as follows: + = Character present, ± = Character weakly developed or tendency, a = present in a few species.

** Numbers in parenthesis are uncommon. In the case of isobilateral leaves, the number refers to the adaxial side only.

Fuchsia and *Hauya*, in which they are confined to the abaxial epidermis; and *Circaea* and *Lopezia*, in which both situations occur. In the Onagreae, stomata were lacking from the adaxial epidermis only in one sample of *Calylophus* and a few of *Clarkia*.

Trichomes are always simple, mostly unicellular, elongate and tapering to a point. They may be slightly expanded or constricted at the base. Bi-cellular trichomes were noted only in *Fuchsia lycioides*, *Ludwigia peruviana*, and *L. lagunae*. All trichomes in the family are usually thick-walled near the base and may or may not be lignified. Neighboring epidermal cells are not modified into buttresses. Trichome surfaces are smooth in many genera (at 400× magnification) but also occur with numerous types of surface features that do not seem readily to fall into a systematic pattern. The surface features are of the same magnitude

TABLE 1. Continued.

Stomata on Adaxial Epidermis	Stomata on Abaxial Epidermis	Styloids or Prismatics	Druses	Coarse Raphides	Fine Raphides	Horizontal, Mid-mesophyll	Random Position	Vertical in Palisade	Crystal Sheaths:	Absent	Thin	Thick	Elongate	Crystals Gum-replaced
+	+	a	+	+	+	+				+				
	+	+	+		+	+						+	+	
a	+				+	+	+	+		+	+	+	+	+
	+			+	+	+	+	+			+	+		
a	+				+	+	+			+	+	+	+	
+	+			a	+	+	+	+		+	+	+	+	±
+	+			a	+	+	+					+		+
+	+	+		+	+	+						+		
+	+		a	a	+	+	+	+		+	+	+		
+	+			+	+	+	+	+				+	+	
+	+				+	+		+				+	+	
+	+				+	+				+	+			
+	+			+	+	+	+					+		
+	+			+	+	+		+		+	+	+		
+	+			+	+	+	+					+		
+	+			+	+	+								
+	+			+	+	+		+		+	+	+	+	
+	+			+	+	+		+		+		+		

as pollen sculpturing and can be called rugulate, striate, or erose-rugulate with sculpturing patterns arranged in wavy vertical lines. Surface structural elements may be scabrate, gemmate, verrucate, or echinate in larger or more minute sizes (less than 1 μm) and uniformly dispersed. A thorough study of trichome surfaces in the Onagraceae using scanning electron microscopy would probably produce systematically valuable data.

The mesophyll in leaf transection may show a clear differentiation between a well-formed palisade and the adjacent spongy layer or there may be a gradual transition between the two epidermal layers. This distinction is noted in Table 1 as "mesophyll well- or mesophyll poorly differentiated." There is generally a correlation between small midribs with small midveins and poor mesophyll differentiation. Palisade cells consistently constitute only one adaxial layer in *Cir-*

caea, *Fuchsia*, *Hauya*, *Heterogaura*, and *Ludwigia* but may be one or two layers in different species of other genera. Many studies on the ecological anatomy of tree species (e.g., Hanson, 1917; Drury, 1973) indicate that the degree of mesophyll differentiation is highly dependent on the degree of exposure to the sun. My experience with the Onagraceae suggests that, for several reasons, this is not an important factor. First, all of the herbaceous plants studied seem to grow normally in full sun with all leaves receiving a similar exposure. Secondly, multiple samples of a number of species have shown no significant structural differences in the mesophyll. Finally, those genera that would be most likely to show palisade layer differences due to shading in a forest environment (*Hauya*, *Fuchsia*) were uniform in my sample in having leaves with single palisade layers. Certainly the condition of having only one adaxial layer in the mesophyll must be primitive in the family, judged from the correlation with other features.

All petiolar traces and leaf midveins in the family have, abaxial to the xylem, a continuous band of primary phloem. In addition, all leaves with large conspicuous midveins have additional patches of phloem adaxial to the xylem. The term bicollateral as commonly described (Esau, 1965, p. 368) would seem to apply but is probably not appropriate. The adaxial phloem is not proximal to the protoxylem but is separated from it, often by a thick band of parenchyma. In those more primitive genera where deep semicircular traces are found (*Fuchsia*, *Ludwigia*, *Lopezia*, *Hauya*) the adaxial phloem may be scattered as random patches in the ground tissue within the semicircle. In genera with broad arcs (*Gaura*, *Oenothera*), the adaxial phloem is best developed lateral to the edges of the xylem and is generally not continuous across the trace. Secondary veins are usually collateral and surrounded by parenchymatous sheaths that differ little from spongy mesophyll in most species. Esau (1980, p. 181) has pointed out that almost no studies of dicotyledonous metaphloem patterns have been done, leaving the homologies of that tissue almost unknown.

Extraxylary fibers are found only in *Fuchsia*, *Hauya*, and *Ludwigia*. Both species of *Hauya* have a midvein surrounded by a layer of fibrous cells that are thick-walled but not birefringent. Fibrous tissue of the secondary veins extends transcurrently to both epidermal layers. Within *Fuchsia* only *F. arborescens* has been noted so far as having extraxylary fibers. *Ludwigia peruviana*, *L. polycarpa*, and *L. suffruticosa* have a sheath of fibers abaxial to the midvein phloem as well as sheaths surrounding the secondary veins. In Safranin-Fast Green preparations of the leaves of the three genera that show good differentiation and red-stained xylem, the extraxylary fibers stain a distinctive blue-green. In *Fuchsia* and *Ludwigia*, the fibers as well as the xylem are strongly birefringent.

Sclereids and laticifers are absent from the Onagraceae but calcium oxalate crystals are present in a diverse assortment of types. All genera contain packets of raphides but these vary markedly along systematic lines in orientation, in coarseness, and in covering. In *Ludwigia*, the raphides are surrounded by thin, non-staining membranes and are randomly or horizontally disposed in the mesophyll. In all other genera, the fine raphides are thinly or heavily sheathed in an amorphous material that has a strong affinity for Safranin-O. The raphide packets are horizontally or randomly (obliquely) oriented in the mesophyll or vertically oriented in the palisade layer. In the latter condition they are often the size and

shape of palisade cells in some species of *Fuchsia*, *Lopezia*, *Camissonia*, *Gayophytum*, *Gaura*, *Clarkia*, *Oenothera*, *Stenosiphon*, and *Epilobium*. In a few species of *Lopezia*, *Epilobium*, and *Boisduvalia*, the raphides may be totally replaced with the red-staining "gum," producing bodies having a strong superficial resemblance to sclereids. Coarse raphides occur in species of nine genera and often in the same tissues where the finer type is found. Prismatics or single rhombohedral crystals occur in a few species in the genera *Ludwigia*, *Gongylocarpus*, and *Hauya*. In *Ludwigia leptocarpa* the prismatics equal the leaf thickness in length and may be termed styloids. Druses are not common in the family but are abundant in a few species of *Ludwigia*, *Hauya*, and *Gaura*. The genus *Ludwigia* includes all forms of calcium oxalate crystals.

Angularly thickened collenchyma may be present or absent beneath epidermal layers in the midrib zone. Its presence is not particularly a function of leaf size or robustness nor was any systematic relationship discerned in this study.

TRENDS OF SPECIALIZATION

When interpretated carefully, leaf histology does have considerable systematic value as can be attested by such recent studies as Dickison (1975) on the Cunoniaceae, Drury (1973) on the Senecioneae-Compositae, or Dickison (1969) on the Dilleniaceae. The principal difficulty with leaf histology is that its trends of specialization are not yet well anchored in the fossil record. Recent stratigraphic studies of angiosperm pollen and leaf architecture (Doyle & Hickey, 1976) have demonstrated an increasingly regular and organized leaf architecture as one moves toward the present in the fossil record. In addition, Hickey and Wolfe (1975) showed that leaf architecture may become reduced in complexity within specific groups such as the Dilleniidae. For leaf histology, it will be necessary for the time being to rely on correlation of character states with other better known trends in well studied plant families such as the Onagraceae. In spite of Stebbins' (1974) caveat that correlations may be spurious if the character states being correlated are not functionally related, it should be possible, using the Onagraceae, to contribute to our knowledge of histological trends of specialization without making too many assumptions. As a result of much previous work we have documented morphoclines from wood, flowers, pollen, flavonoids, chromosomes, and breeding systems. Before discussing the trends in leaf histology, it is necessary to comment on the following inferences, which seem warranted based on this literature. These arguments are critical to any understanding of leaf specialization within the Onagraceae.

The family probably originated in South America in the late Cretaceous from ancestral stock related to other Myrtalean families (Raven & Axelrod, 1975; Raven, 1979). These families are presently distributed overwhelmingly in the southern hemisphere.

Within Onagraceae, *Ludwigia* clearly represents a distinct phylogenetic line, or one that is, in Hennigian terms, the "sister group" of all other Onagraceae (Eyde, 1981). Both it and *Fuchsia* have their greatest diversity and their most primitive species in South America at the present time, this relationship being consistent with the probable place of origin of the family, as just hypothesized.

Two other of the tribes that have been regarded as relatively generalized, those constituting the single genera *Hauya* and *Lopezia*, are restricted to Mexico and Central America, regions easily accessible to migration from South America at an early date (cf. Raven & Axelrod, 1975). *Circaea*, the only genus of the tribe Circaeeae, was probably an early offshoot of one of these tribes. *Circaea* is restricted to the remnants of the Arcto-Tertiary Geoflora and best represented in temperate eastern Asia, with two species and a hybrid in North America and Europe. *Circaea* has a fossil record from Eurasia from the Oligocene onward (Eyde & Morgan, 1973).

The remaining tribes of the family, Onagreae, with ten genera, and Epilobieae, with two, appear to have originated in western North America in association with the development of the Madro-Tertiary Geoflora, perhaps in mid-Tertiary times (Raven, 1976; Raven & Axelrod, 1978).

The longest vessel elements (over 500 μm) are found in species of *Fuchsia*, *Ludwigia*, and *Hauya* (Carlquist, 1975). Most genera of the Onagreae and Epilobieae have vessel elements that are generally considerably shorter in both mean and range. The most extensively developed secondary xylem in the Onagraceae is found in *Fuchsia* and *Hauya*, with somewhat smaller woody stems found in a few species of *Ludwigia*, *Lopezia*, and *Epilobium*, very little wood in the Onagreae, and none in *Circaea*. Since none of these show any signs of having a secondarily derived wood anatomy (Carlquist, 1975), the xylem trends, along with biogeographic data, are possibly the best arguments for the vegetative primitiveness of *Fuchsia*, *Ludwigia*, *Lopezia*, and *Hauya*. In leaf architecture (Hickey, 1980, this symposium), *Fuchsia* appears to be the most generalized and has the best developed tooth and vein architecture. All other genera appear to constitute a reduction series. Interxylary phloem, certainly an advanced feature, is lacking in *Ludwigia*, *Fuchsia*, and *Hauya*, and present in the more advanced *Lopezia*, Onagreae, and Epilobieae (Carlquist, 1975). The latter two groups lack stipules, another advanced feature.

Summarizing this material briefly, *Ludwigia* represents a phylogenetic line separate from all other Onagraceae. Among the remainder of the family, *Fuchsia* and *Hauya* are the two least specialized genera, with *Circaea* and *Lopezia* related but clearly more specialized in certain respects, especially those concerned with floral morphology. The two most specialized groups, as judged by any criteria, are certainly the Epilobieae and Onagreae, tribes that might or might not share a common ancestor.

On the basis of the foregoing studies, one can best read the morphoclines in leaf histology of the Onagraceae as an overall reduction in histological complexity. Leaves have become smaller, less vascularized, and the vascularization has changed from a broad semicircle to a short arc. This is related to the less prominent abaxial midrib protrusion, which is probably less necessary for support in smaller leaves. In the three genera where extraxylary fibers occur, they are found in the species which have the largest midveins.

Among cellular inclusions, druse crystals and styloids are present in *Ludwigia* and *Hauya*. In addition, druses occur in *Gaura* and prismatics in *Gongylocarpus*, both of the Onagreae. The ability to make these crystals has apparently been lost in other evolutionary lines of the family. Of the various raphide forms, coarse

TABLE 2. Proposed leaf character state assignments for the Onagraceae*.

Character	Primitive State (0)			Advanced State (1)
Stipules	present			absent
Structure	dorsiventral			isobilateral
Midribs	prominent			reduced
Midveins	semicircle		broad arc (0.5)	short arc
Margins	rounded			thickened edge
Extraxylary fibers	present			absent
Stomata	abaxial only			adaxial also
Trichomes	bi- or multicellular			unicellular
Mesophyll	clearly differentiated			poorly differentiated
Palisade layer	single			double
Adaxial phloem	present			absent
Styloids/Prismatics	present			absent
Druses	present			absent
Raphide texture	coarse			fine
Raphide orientation	horizontal		random position (0.5)	vertical in palisade
Raphide sheaths	very thin (0)	thin (0.3)	thick or long (0.6)	replaced (1)

* Character states of 0 = primitive and 1 = advanced are used in Table 3 to score all genera for all characters listed here. Fractional numbers are values assigned to discernable intermediate states along a single morphocline.

raphides may, for several reasons, be proposed as a transition stage leading to fine raphides. The coarse raphides occur in randomly oriented cells in mid-mesophyll in leaves where fine raphides are also present. Whenever fine raphides are covered with thick and/or elongated sheaths, or are oriented vertically in the palisade layer, the coarse raphides are usually horizontally or randomly oriented in mid-mesophyll and without such other features. The thickening of fine raphide sheaths appears to be a step in a sequence leading to their final replacement by the sheath material. The isobilateral and/or reduced leaves are the type that most commonly have vertical thick-sheathed raphides or gum-replaced raphides in the palisade layers.

Table 2 includes a number of proposed trends of specialization that can be supported by the data. Character state figures are assigned ranging from 0 to 1 with "0" indicating the primitive state. In Table 3, leaves of the genera of Onagraceae are assigned values using the character states and values listed in Table 2. A range of 0 to 1 for a particular genus and character indicates that both character states are present in different species of the genus. Where a total range, such as 1–6 is given (e.g., *Ludwigia*), it is likely that only a few species, if any, would be unspecialized in all or most characters (i.e., have an index of advancement total of "1"). Another species may have all of the advanced states and therefore be classed as a "6." Most commonly, a given species may have various combinations of advanced and primitive states, a circumstance that should be further explored genus by genus. In this paper, the range totals for each genus are given in Table 3 as a means of comparing the genera and as a means of noting the evolutionary depth within the family. Note that larger genera show greater ranges of variation. It can be validly concluded that reduction in leaf structural complexity, the development of isobilateral leaves, and the specialization of crys-

TABLE 3. Leaf histology advancement index for genera of Onagraceae*.

	Stipules	Lamina Structure	Midrib	Midvein	Margin	Extraxylary Fibers	Stomata	Trichomes	Mesophyll Differentiation	Palisade	Adaxial Phloem	Styloids/Prismatics	Druses	Raphide Texture	Raphide Orientation	Raphide Sheaths	TOTAL
Ludwigia	0	0	0–1	0–1	0	0	1	0–1	0	0	0–1	0	0	0–1	0	0	1–6
Fuchsia	0	0	0–1	0–1	0	0	0	0–1	0–1	0	0–1	1	1	0–1	0–1	0–.6	2–9.6
Hauya	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0–.5	.6	2.6–3.1
Lopezia	0	0	0–1	0–1	0	1	1	1	0–1	0–1	0–1	1	1	1	0–1	0–1	6–13
Circaea	0	0	1	1	0	1	1	1	1	0	0–1	1	1	1	0–.5	0–.6	9–11.1
Gongylocarpus	1	0	1	1	0	1	1	1	0	0	1	0	1	0–1	0	.3	8.3–9.3
Epilobium	1	0–1	1	1	0	1	1	1	0–1	0–1	0–1	1	1	0–1	0–1	0–.6	8–14.6
Boisduvalia	1	0–1	1	1	0	1	1	1	0–1	0–1	0–1	1	1	0–1	0	0–1	8–14
Oenothera	1	0–1	1	1	0–1	1	1	1	0–1	0–1	0–1	1	1	0–1	0–1	0–.6	8–15.6
Gaura	1	0–1	1	1	0	1	1	1	0–1	1	0–1	1	0	0–1	0–1	0–1	8–14
Camissonia	1	0–1	1	1	0	1	1	1	1	0–1	0–1	1	1	0–1	0–1	.3–.6	9.3–14.6
Calylophus	1	0–1	1	1	0–1	1	1	1	0–1	0–1	0–1	1	1	1	0–1	0–.6	9–15.6
Clarkia	1	0–1	1	1	0	1	1	1	0–1	0–1	0–1	1	1	1	0–1	0–.3	9–14.3
Xylonagra	1	0	1	1	0	1	1	1	1	0	0–1	1	1	1	0	0–.3	10–11.3
Heterogaura	1	0	1	1	0	1	1	1	1	0	0	1	1	1	0–1	.3	10.3–11.3
Stenosiphon	1	1	1	1	1	1	1	1	0	1	0	1	1	0–1	0–1	0–.6	11–13.6
Gayophytum	1	1	1	1	0	1	1	1	1	1	0	1	1	1	0–1	.6	12.6–13.6

* Character state codes are as listed in Table 2. Higher numbers indicate greater advancement. See text for further discussion.

tals, are changes that have taken place repeatedly in many genera. To postulate otherwise would imply that structural elaboration and reduction have proceeded back and forth, a conclusion that does not harmonize with data from any of the recent monographs that have been done on a number of the genera (e.g., Ramamoorthy, 1980, on *Ludwigia*; Wagner, in prep., on *Oenothera*; Raven & Gregory, 1972, on *Gaura*; Hoch, 1978, on *Epilobium*; Plitmann et al., 1973, on *Lopezia*). In each case, the leaves that would be classed here as unspecialized are placed in the more generalized sections based on comprehensive taxonomic criteria.

INTRAFAMILIAL RELATIONSHIPS

Eyde's (1977, 1981) studies of *Ludwigia* demonstrate that its floral anatomy is distinct from that of other Onagraceae, as mentioned above. Its central and transseptal ovular supplies, unusual nectary position, and ancient fossil record (Eyde & Morgan, 1973) suggest that the genus is a sister group to all other Onagraceae. Leaf anatomy supports this contention. The anatomy of *L. peruviana* (sect. *Myrtocarpus*) as well as that of a few species from sects. *Macrocarpon*, *Oligospermum*, *Humboldtia*, *Ludwigia*, and *Seminuda*, shows an elaborate midrib structure not approximated in any other genus. This is marked by the pronounced and flattened adaxial ridge of the midrib into which palisade mesophyll laterally intrudes. While at least one other genus may have one or another of *Ludwigia*'s features (e.g., druses occurring also in *Hauya* and *Gaura*), its anatomy among the more generalized sections with which it is commonly compared is absolutely distinguishable. In fact, its midrib structure has not been described from any other angiosperm. It should be noted that the species with less elaborate or reduced leaf structures in any genus of Onagraceae cannot generally be diagnosed or assigned to a genus with certainty.

Hauya has been considered to be the basal genus of the Onagreae (Raven, 1964) but is recently considered to belong in its own tribe, Hauyeae (Raven, 1979). Leaves of the genus bear no resemblance to any of the Onagreae, all of which are much more reduced (Table 3). Its arborescent habit, lack of adaxial stomata, and lack of a prominent adaxial midrib ridge separate it from *Ludwigia*. Separation from *Fuchsia* is not as easy. *Hauya*'s styloids and druses are not found in *Fuchsia* but the two genera are otherwise generally similar, especially in floral morphology and habit, and, with *Ludwigia*, are unique in Onagraceae in lacking interxylary phloem. Shoot apex studies (Keating, in prep.) indicate that *Hauya* has a leaf primordium configuration similar to that of *Fuchsia*, but differs in two important respects. Its young leaf primordia (in both species) show basal concrescence and the stipules emerge at a lower level. Otherwise, the shoot apices of the two genera closely resemble each other. The basic chromosome number in *Hauya* ($x = 10$), and possibly also the chromosome morphology as seen in mitosis (Kurabayashi et al., 1962), are derived as compared with that of *Fuchsia*, *Circaea*, and primitive species of *Lopezia* ($x = 11$).

It has been suggested (D. Boufford, pers. comm.) that *Fuchsia* may share an immediate common ancestor with the circumboreal *Circaea*, a genus that has structurally reduced leaves and could therefore have been derived from a *Fuch-*

sia-like ancestor. *Circaea* has had a fossil record since the Oligocene and its distinct flavonoid biochemistry suggests no clear relationships (Boufford, Raven & Averett, 1978). Its leaf structure suggests a *Fuchsia*-like plant that has lost a large midvein and all crystals but raphides. The relationship does not appear to be direct, and the similarity is probably based on shared ancestral (generalized) features that do not reflect an immediate common ancestor. In other words, the demonstrated similarities neither prove nor disprove a direct relationship between *Fuchsia* and *Circaea*. The mitotic chromosomes of primitive species of *Lopezia*, with a gametic chromosome number of $n = 11$, closely resemble those of *Fuchsia* and *Circaea* (Kurabayashi et al., 1962).

Lopezia shares with *Ludwigia*, *Fuchsia*, and *Hauya* the presence of stipules and a large midrib and midvein in the larger-leaved species, but it shows several marked advances, including the reduced stamen number (2), highly zygomorphic flowers, and presence of interxylary phloem. The extraxylary fibers are lacking as are all crystal types except fine raphides. In these respects it is similar to *Circaea* but virtually all additional features examined serve to separate the two. *Lopezia* has one or two palisade layers, interxylary phloem in the wood (Carlquist, 1975), and heavy gum sheaths around raphides in almost all species examined. Horizontal raphide sheaths may extend far beyond the crystals to a total length of 240 μm in *L. suffrutescens*, *L. grandiflora*, and *L. riesenbachia*. In some other species, the vertical gum sheaths in the palisade layer seem to contain no raphides at all but instead assume the appearance of dense, red-staining macrosclereids. With these features, *Lopezia* also seems to have had an isolated, separate evolutionary development within the family. Like *Circaea*, it shares many features with the postulated common ancestor of *Fuchsia* and *Hauya*.

The tribe Epilobieae, containing ca. 200 species of *Epilobium* plus *Boisduvalia*, is clearly a natural group on the basis of its morphology, its dotlike heteropycnotic chromosomes and its habit (in most species) of shedding pollen as tetrads (Raven, 1976). Leaf anatomy is generally quite reduced causing difficulty in discerning morphoclines let alone determining trends of specialization. Specimens of *Boisduvalia* and *Epilobium* are quite similar in their array of variation. *Epilobium suffruticosum* (sect. *Cordylophorum*) is alleged to be similar to the ancestral type (Raven, 1976) on the basis of its suffruticose habit, floral morphology, and chromosome number. This species has a distinctive isobilateral leaf, a striate cuticle, and a centric organization of palisade around a very small midvein, features that give the leaf a very xeromorphic appearance despite the species preference for permanently moist places. Raven (1976) and Raven and Raven (1976) have proposed that the extinct hypothetical ancestors of *Epilobium* were diploid xerophytes. If this is true, many of the dorsiventral-leaved species of other sections may possibly have been derived from ancestors with isobilateral leaves. Extremely divergent within *Epilobium* is sect. *Chamaenerion* (cf., Keating, Hoch & Raven, 1982). *Epilobium angustifolium* and *E. latifolium* show dorsiventral structure and large midribs (for the genus) with well developed adaxial phloem over broad midrib arcs. Such anatomy suggests that sect. *Chamaenerion* may be a sister group to the other five sections and may have developed from a primitively mesomorphic ancestor. Alternatively, *E. dodonaei* and *E. fleischeri* of sect. *Chamaenerion*, with their very reduced vasculature and isobilateral struc-

ture, may be primitive ones similar to *E. suffruticosum*. *E. angustifolium* and *E. latifolium*, however, show no signs of being secondarily woody according to Carlquist's (1962) criteria. The two sections of *Boisduvalia* are more similar to *Epilobium*, excluding sect. *Chamaenerion*, than that section is to any other member of the tribe. Peter Raven (pers. comm.) has suggested that the sections of *Boisduvalia* may have been (independently) derived from *Epilobium*, and perhaps should not be treated as generically distinct from it; whereas perhaps *Chamaenerion*, with its possibly primitive habit of shedding its pollen singly, may be the "sister group" of all other Epilobieae.

The Onagreae comprises a group of ten genera that are restricted as native plants to the New World and best represented in western North America (Raven, 1979). Most of the genera have at least one or more distinctive leaf structures but leaves from perhaps the majority of the more derived species could be placed in any of a half dozen genera. Group 1 Onagreae (Raven, 1979) consists of *Camissonia*, *Gayophytum*, *Gongylocarpus*, and *Xylonagra*. *Camissonia*, with 61 species, is the largest genus and its leaves contain midribs of various size and structure. Each of the four genera has one or more distinctive but not diagnostic features among its species. *Camissonia* has raphide gum sheaths up to 300 μm long as does *Gayophytum*. *Xylonagra* has boldly tuberculate trichomes, and *Gongylocarpus* has prismatic crystals.

Group 2 Onagreae consists of *Calylophus*, *Clarkia*, *Gaura*, and *Heterogaura*. Of these, *Gaura* alone is strikingly distinctive. The largest leaves tend to have a pronounced rounded midrib adaxially and abaxially. The broad arc midvein and its surrounding ground tissue is flanked by a concave mesophyll laterally lining the midrib zone. Best development is seen in *G. parviflora* (sect. *Schizocarya*), *G. lindheimeri*, and *G. longiflora* (both sect. *Gaura*). *Clarkia* and *Heterogaura*, clearly closely related on other grounds, are absolutely coincidental anatomically. Each has a very reduced midrib and midvein structure. *Clarkia concinna* has a very short, curved, striate, and papillate trichome type and raphides often occurring in paired bundles in ovate-outlined heavy sheaths. *Calylophus* has short rounded trichomes, and may have striate-ridged cuticle over leaf margins like *Gaura*. In contrast to *Gaura*, however, *C. berlandieri* has a mechanical zone at the margin (probably collenchyma) reminiscent of *Stenosiphon*. Its isobilateral mesophyll is centrically arranged around a small midrib as in *Epilobium suffruticosum*, however.

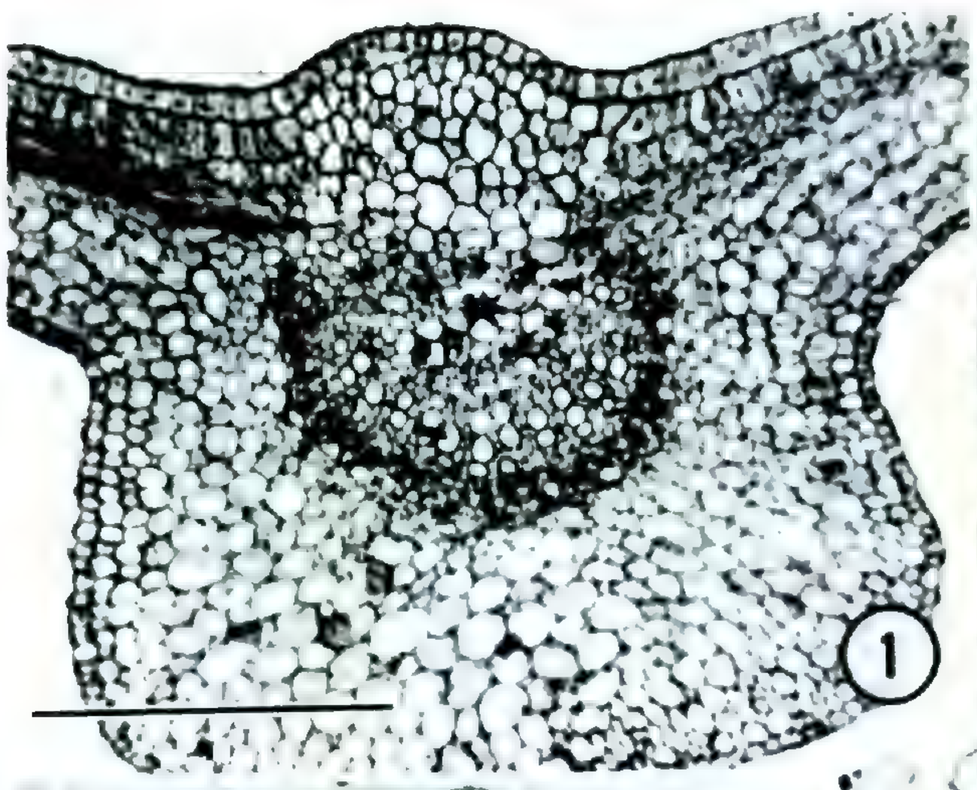
Group 3 Onagreae, with *Oenothera* and *Stenosiphon*, shows distinctive anatomy. Several patterns are found in *Oenothera* that range from the most massive leaf structure in the family (*O. macrosceles*, *O. grandiflora*) to thin and structurally reduced ones (*O. mendocinensis*). There is a tendency for the leaves with large midribs and broad arc midveins to be in the more primitive sections (Warren Wagner, pers. comm.), but my sample of this complex genus is insufficient to establish trends at present. *Stenosiphon linifolius* is quite easily distinguished from any *Oenothera* species with its isobilateral leaf containing pronounced and rounded midrib protrusions of equal height on both surfaces. The mesophyll within the midrib zone forms a lateral concave boundary against the midrib ground tissue. Its margin has a zone of thickened cells extending beyond the mesophyll a distance equal to the leaf thickness (310 μm). *Oenothera macrocarpa* (sect.

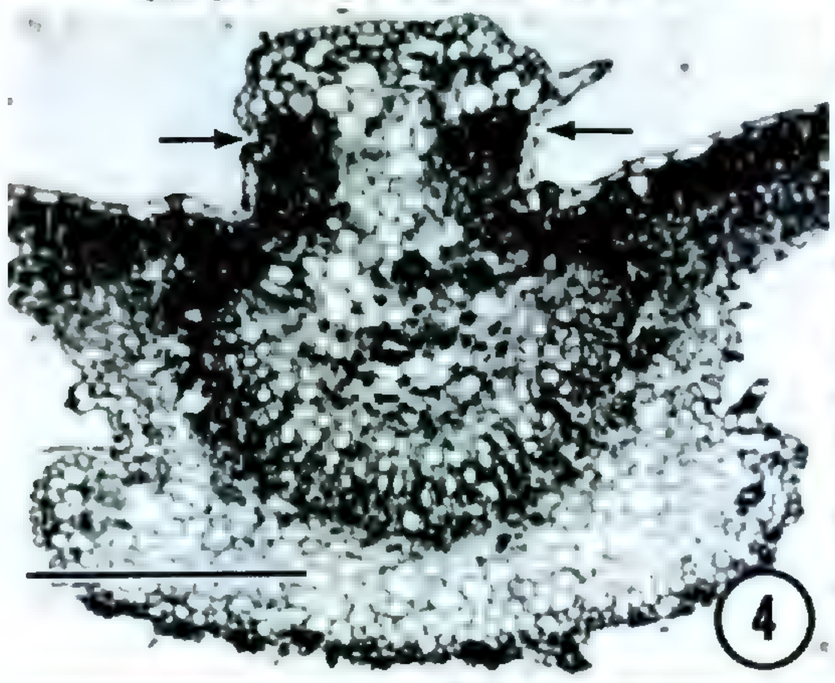
Megapterium) is the most similar (including midrib and margin anatomy) but *Stenosiphon* has a more strikingly symmetrical midrib. Also quite similar are the above mentioned *Gaura* species but the genera can be distinguished. The adaxial phloem band in *Stenosiphon* is separated from the xylem by the midrib ground tissue while in *Gaura* the adaxial phloem is quite close, perhaps truly bicollateral on the midvein. In addition, the margins of *Gaura* leaves have a sharply striate cuticle over an epidermis that is directly adjacent to mesophyll tissue. *Stenosiphon* margins have a smooth surface over a zone of marginal mechanical tissue. I believe, therefore, that the other structural similarities have a parallel origin.

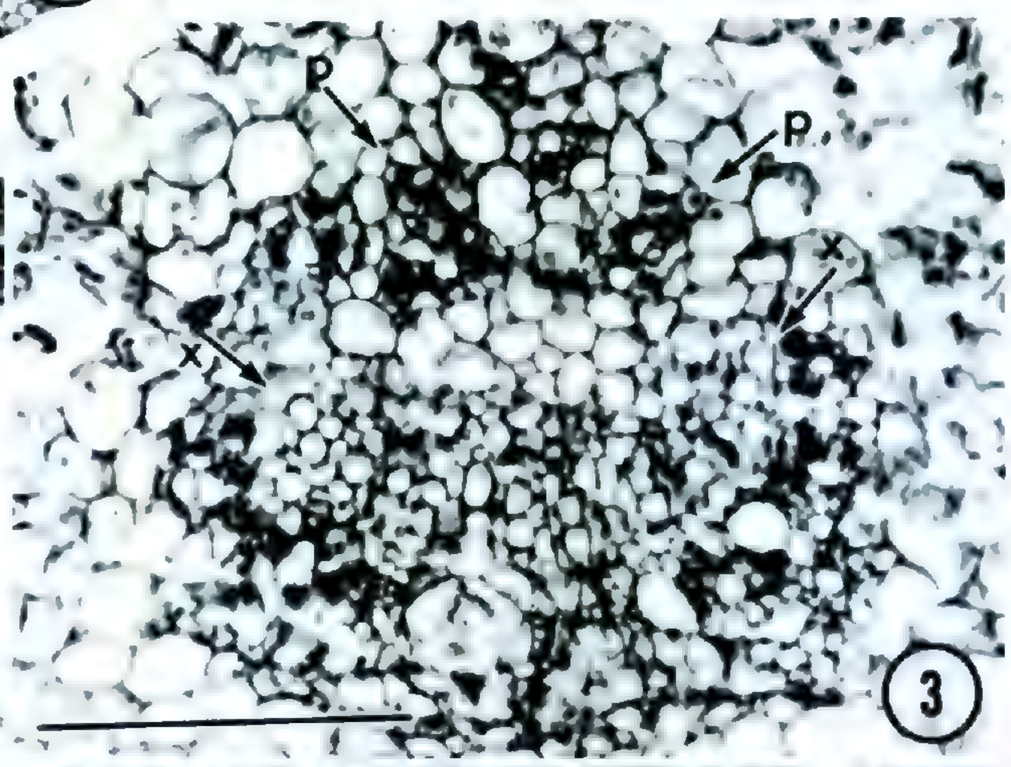
The principal question regarding the Onagreae remains whether evolutionary lines can be detected or whether the ten genera represent mostly isolated end lines of similar levels of advancement. With the data available, the question must remain open. A distinct and limited array of character states occurs in the Onagreae but not in any clear pattern. The character state analysis attempted here using punched cards and correlation matrices produced no discrete clusters, the character states showing instead almost a reticulate pattern among the genera. These leaves appear structurally simplified and efficient, carrying little in the way of remnants of a structurally more elaborate ancestry. The hypothesis of a common origin remains viable but so many of the genera have shown similar reduction sequences that much more refined data and analysis will be needed before the lines will be sorted out.

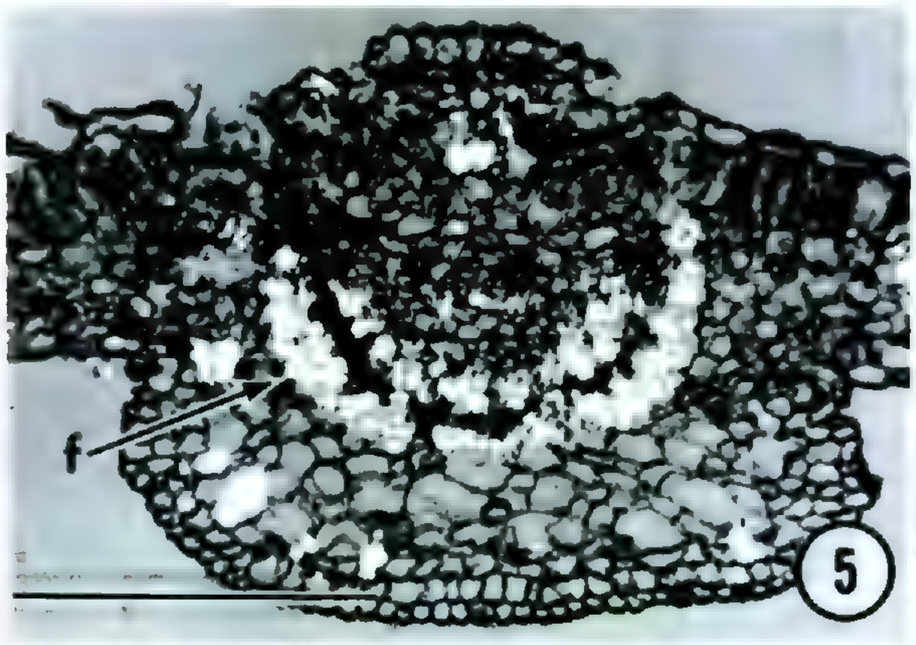
INTERFAMILIAL RELATIONSHIPS

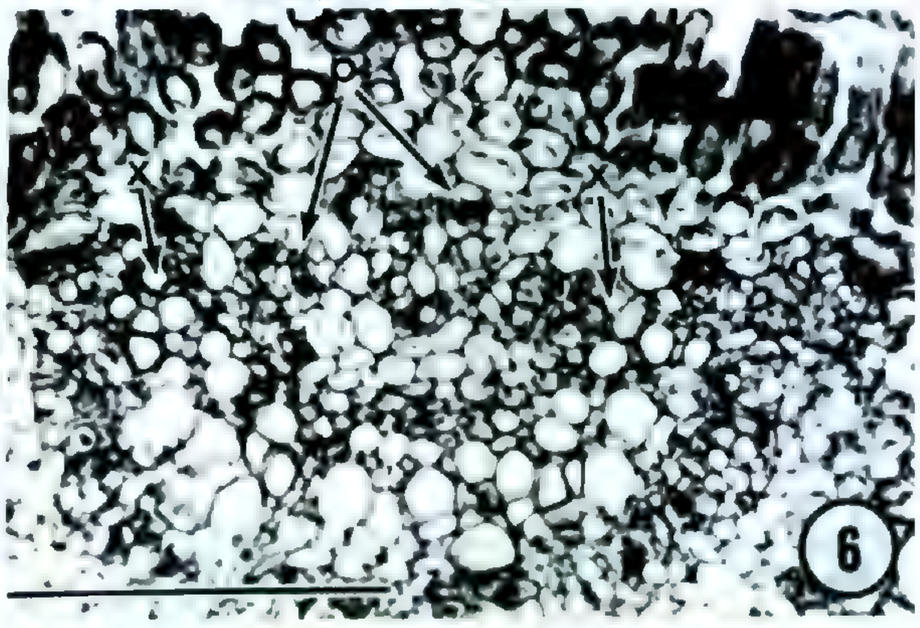
Carlquist (1975) stated that ". . . [wood] anatomical features prove unusually decisive in establishing relationships of the Onagraceae." He stated that affinities seem greatest with the Lythraceae, Punicaceae, Sonneratiaceae, Crypteroniaceae, Combretaceae, and less strongly, with Melastomataceae. Unfortunately, with the present data available on other Myrtalean families, leaf anatomy proves unusually indecisive at the moment. The leaf structure of the other families of Myrtales, including their petiole anatomy, is generally much more complex than that of the Onagraceae. This would appear to provide corroboration for the idea that the Onagraceae represent a reduction series in these respects. Perhaps the most intriguing piece of data is the anatomy of the hydathodal tooth of the Onagraceae, which is also present in Lythraceae. The striking similarity of these teeth to the same feature found in several genera of woody Saxifragaceae by Stern (1974, 1978) and Styer and Stern (1979a, 1979b) may imply an ancestry directly out of the ancestral Saxifragales (of Takhtajan, 1969) for the Onagraceae, Lythraceae, and thus Myrtales in general. Until studies of Myrtalean leaf structure, now underway, are completed, further speculation will provide no useful insights.

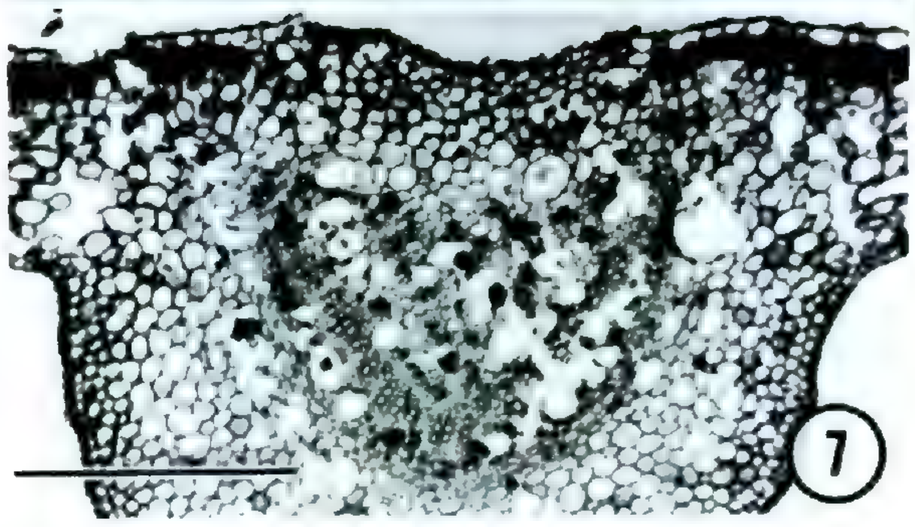


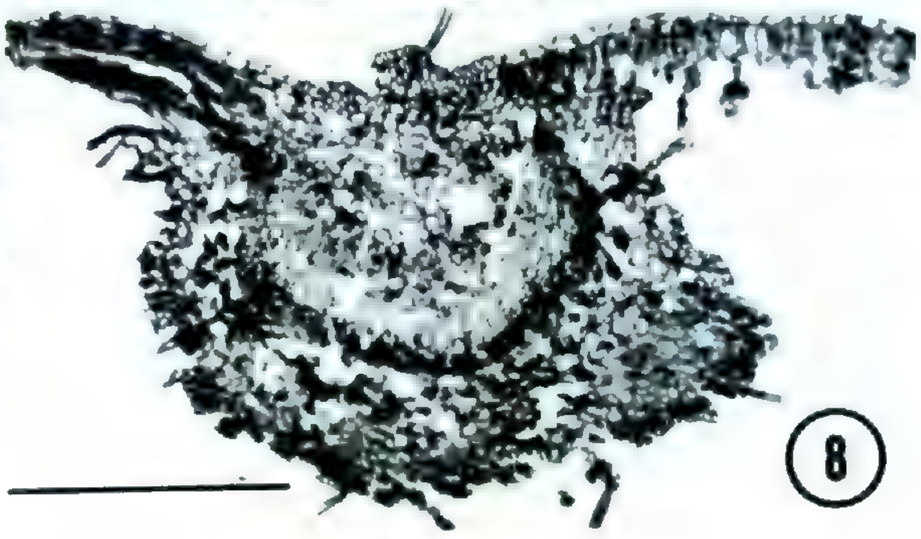




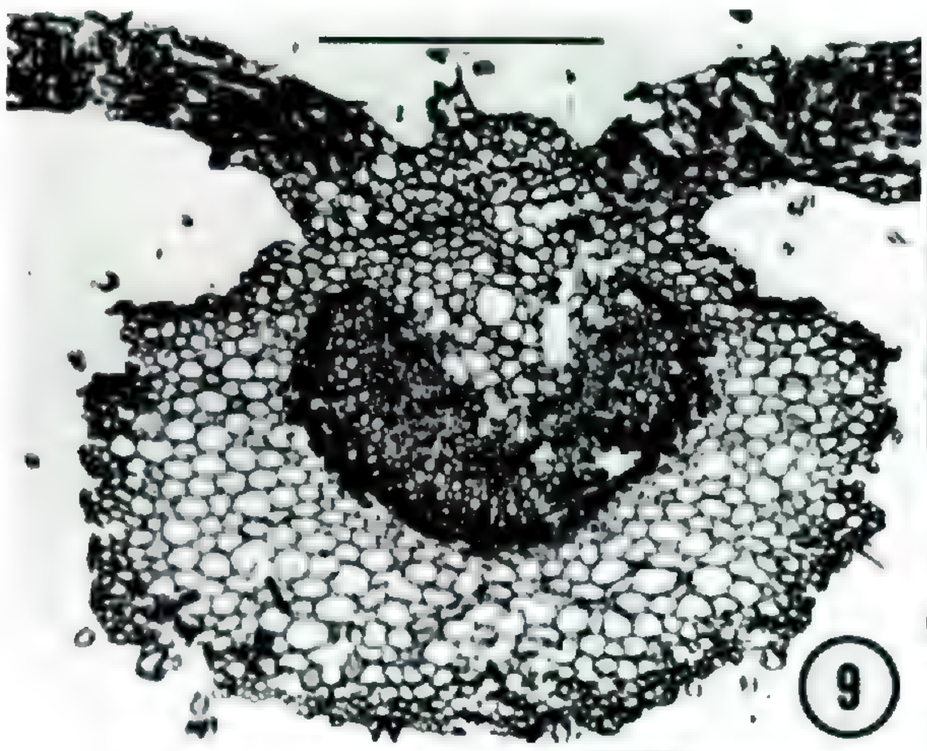


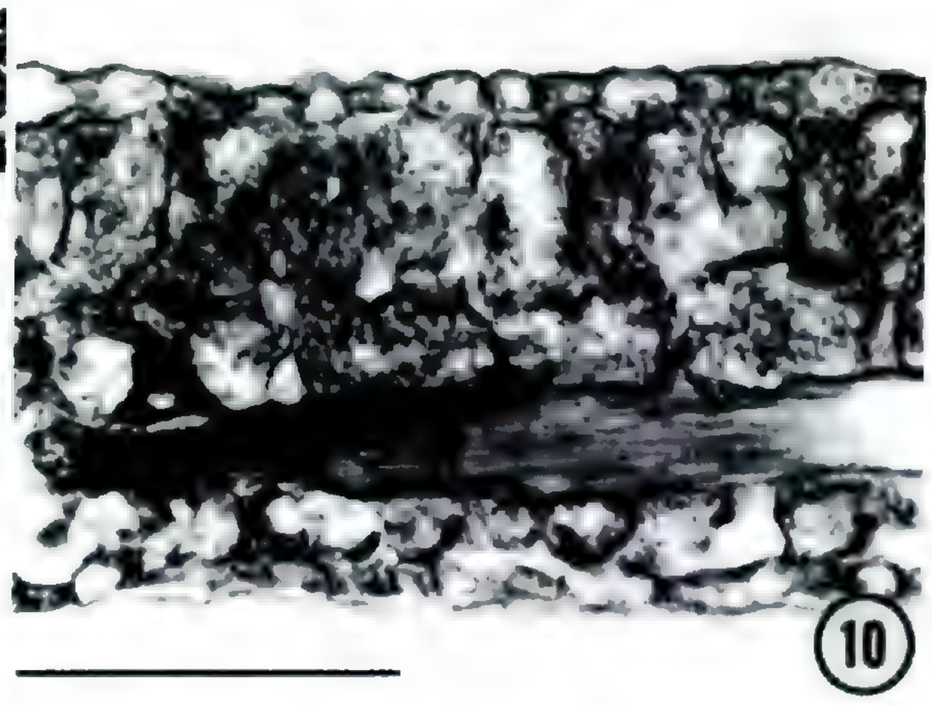


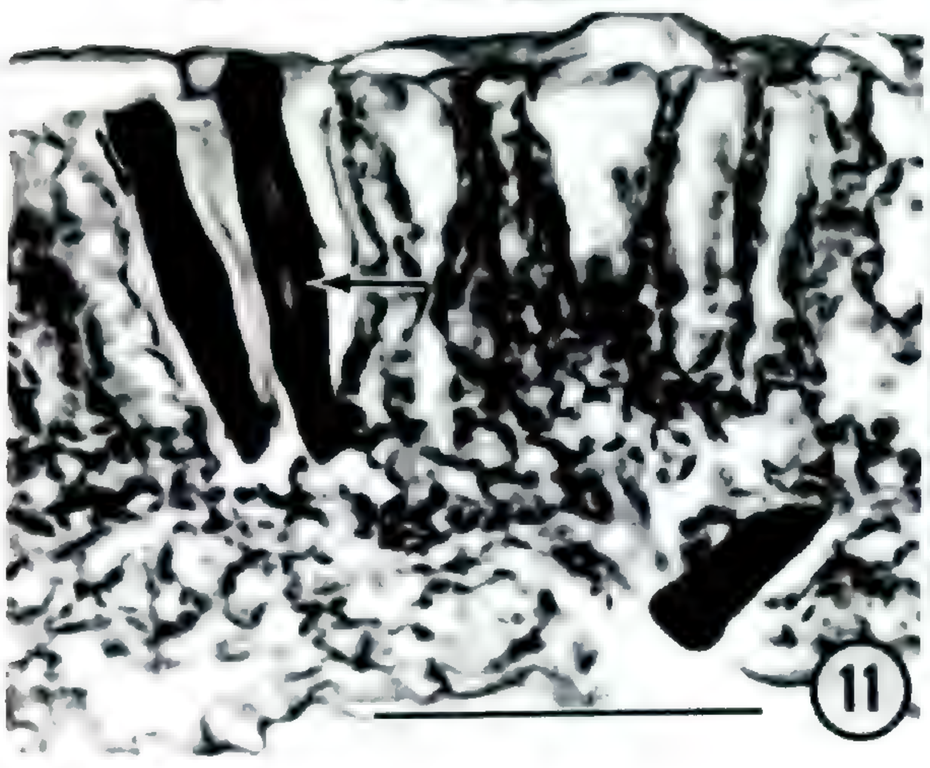


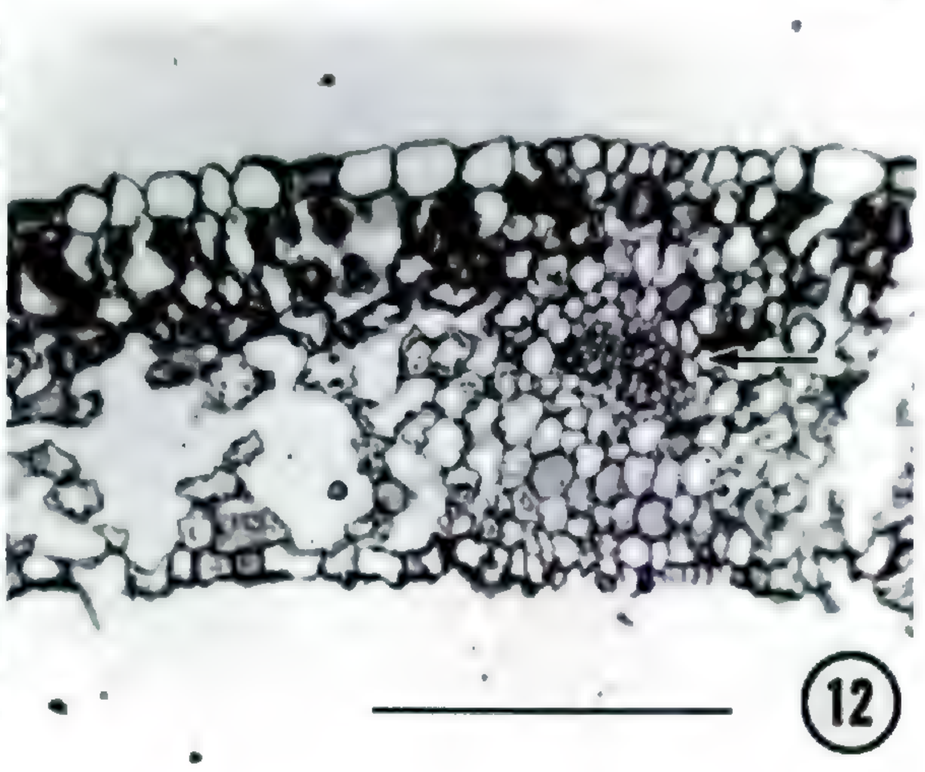


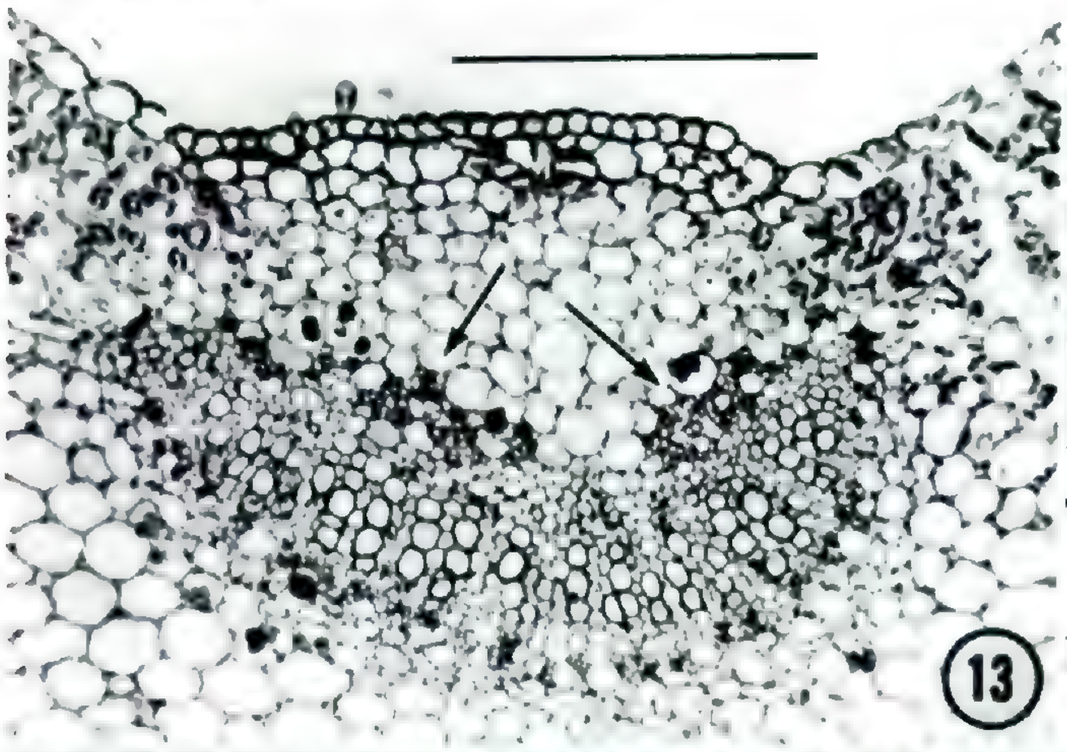
FIGURES 1–8. Leaf cross sections of Fuchsieae, Jussiaeeae, and Hauyeae.—1. *Fuchsia arborescens*, young leaf midrib. The vascular trace is semicircular.—2. *F. boliviana*, lamina section with raphide cell. Raphides are surrounded by a heavy elongated gum sheath.—3. *F. ravenii*, section of broad arc midvein showing adaxial phloem zone (p-arrows) well above the ends of the xylem (x-arrows).—4. *Ludwigia peruviana*, midrib section with semicircular vascular trace and mesophyll tissue in the adaxial ridge (arrows).—5. *L. suffruticosa*, midrib section under polarized light. Note light xylem semicircle surrounded by the dark band of abaxial phloem. Extraxylary fibers (f-arrow) surround the phloem.—6. *L. peploides*, midvein section with xylem semicircle (x-arrows) and adaxial phloem patches (p-arrows).—7. *Hauya heydeana*, midrib section showing semicircular vascular trace.—8. *H. elegans*, midrib section showing large semicircular vascular trace. Scale lines equal 500 μm for Figs. 4, 7, 8; 250 μm for Figs. 1, 5; 100 μm for Figs. 2, 3, 6.

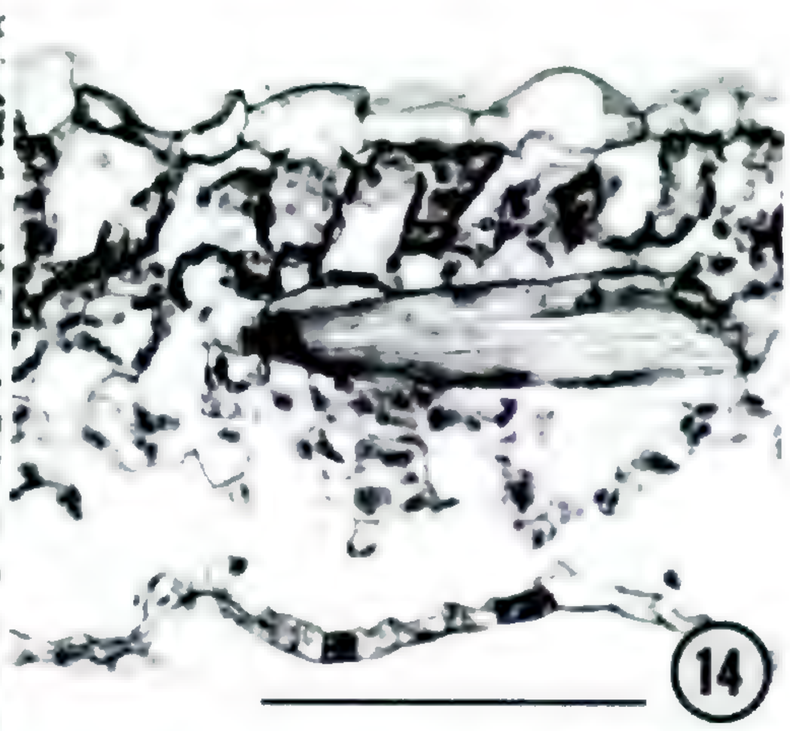


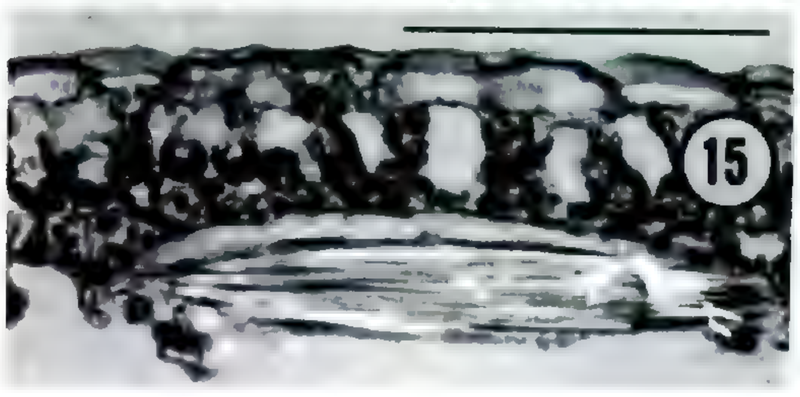


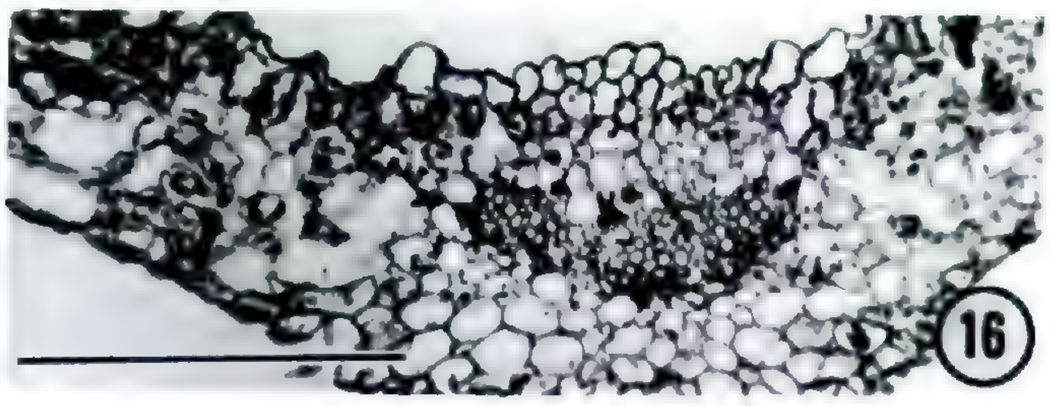




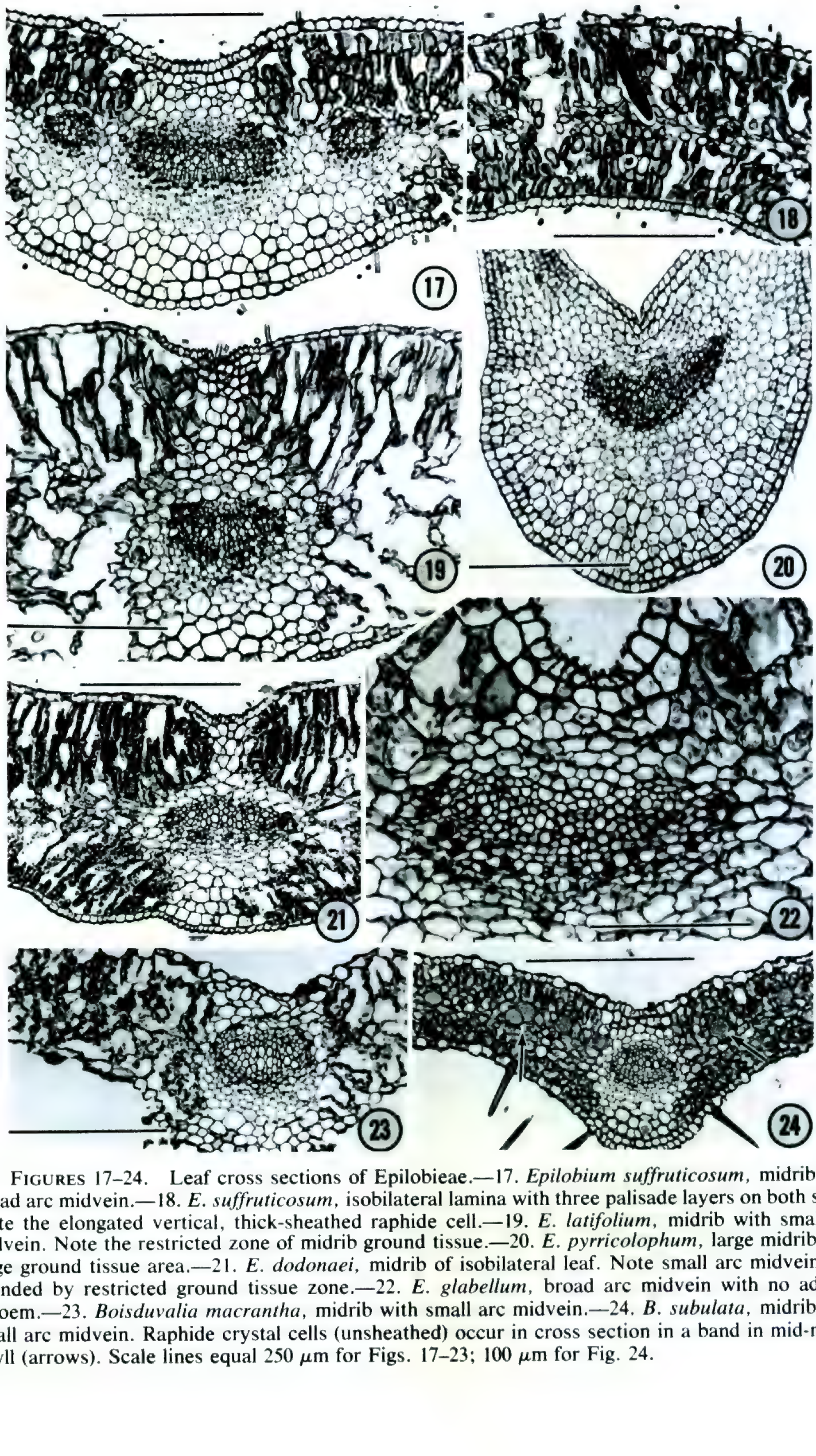




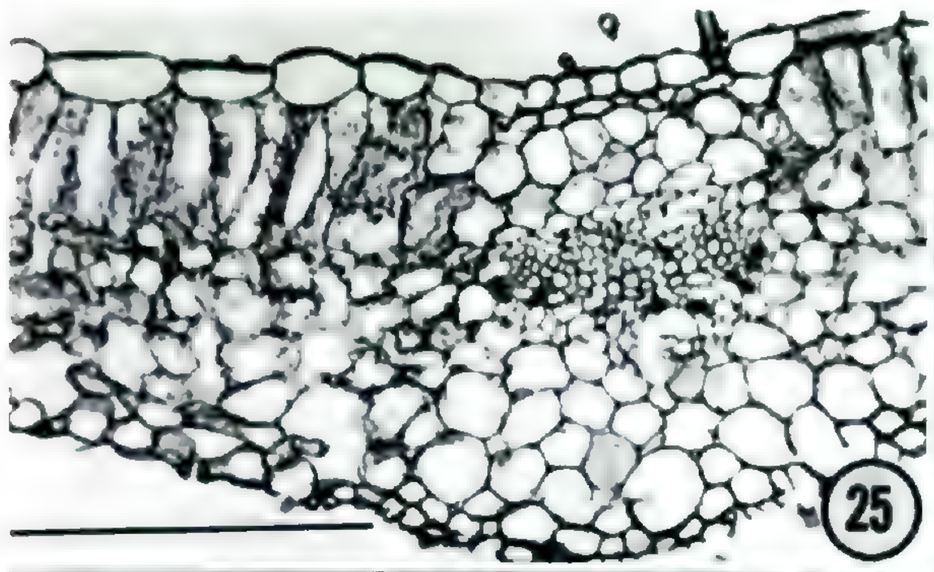


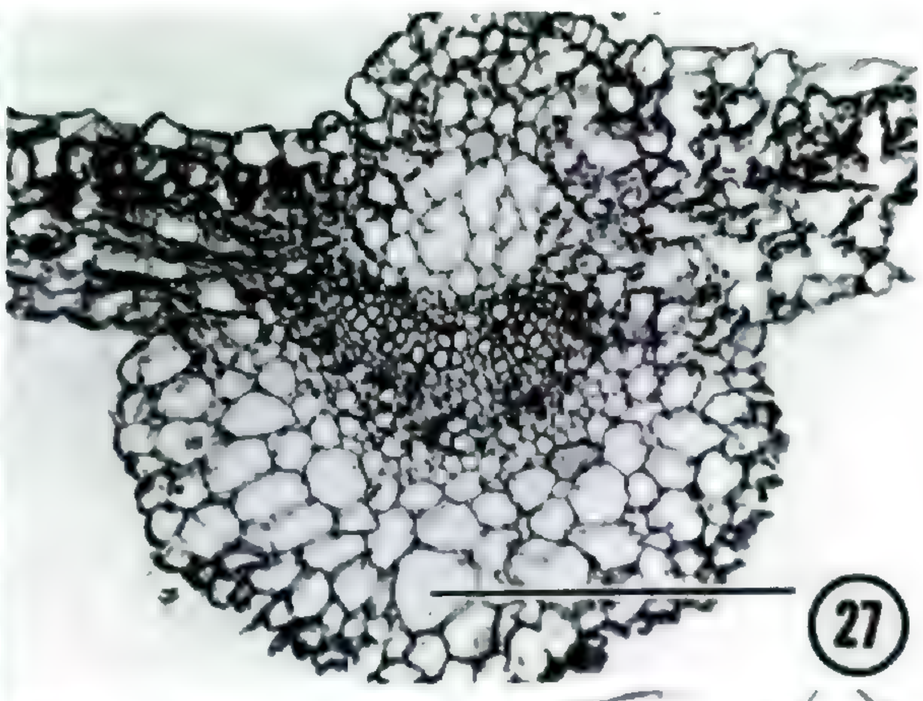


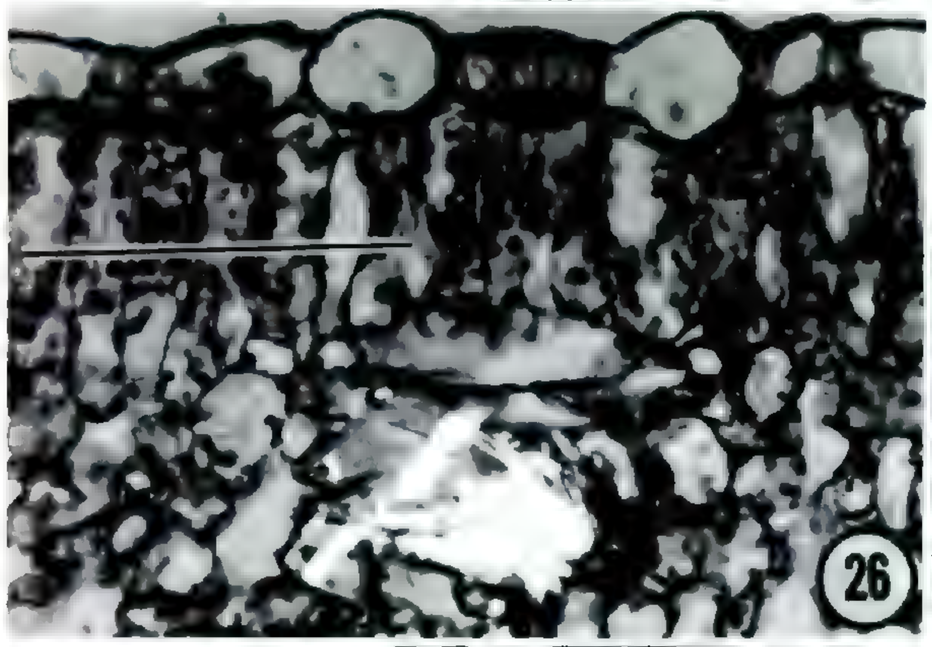
FIGURES 9–16. Leaf cross sections of Lopezieae and Circaeeae.—9. *L. semeiandra*, midrib section. Note semicircular vascular trace and overall rounded appearance of the midrib outline.—10. *L. riesenbachia*, lamina with thick, elongated raphide sheath covering fine raphides.—11. *L. racemosa*, lamina with two thick raphide sheaths in the palisade. Raphides are barely visible (arrow).—12. *Circaea cordata*, short arc midvein immersed in a midrib that shows no adaxial or abaxial distention. Note short arc midvein (arrow).—13. *C. lutetiana*, midrib and midvein. Note the adaxial phloem (arrows) formed close to the protoxylem.—14. *C. erubescens*, lamina showing fine raphides horizontal in mid-mesophyll. Note the thin sheath.—15. *C. lutetiana*, adaxial half of lamina with unsheathed fine raphide bundle under polarized light.—16. *C. erubescens*, small midrib with broad arc midvein. Midvein-mesophyll boundary is poorly differentiated and no adaxial phloem is present. Scale lines equal 500 μm for Fig. 9; 250 μm for Figs. 12, 13, 15; 100 μm for Figs. 10, 11, 14, 16.

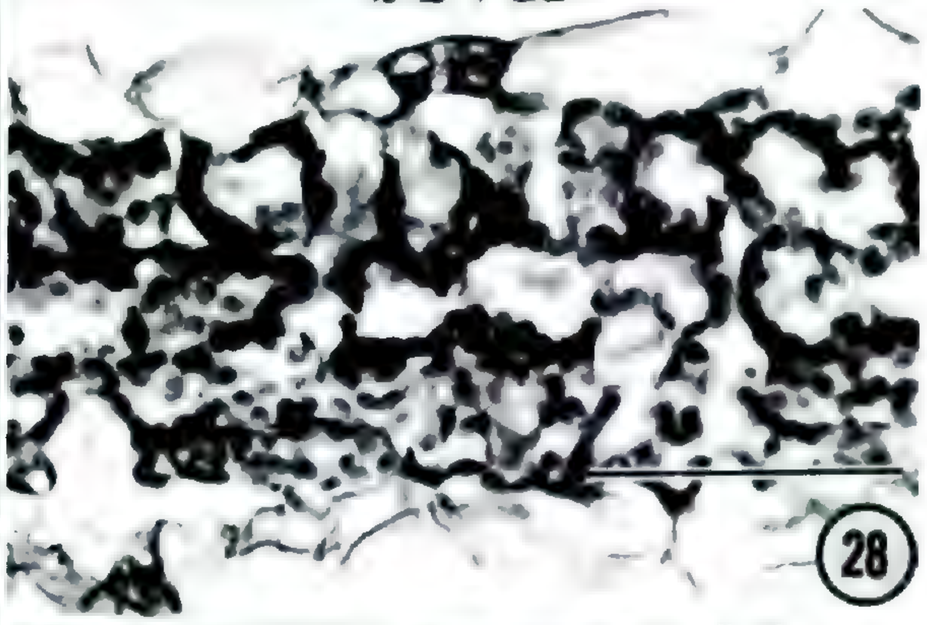


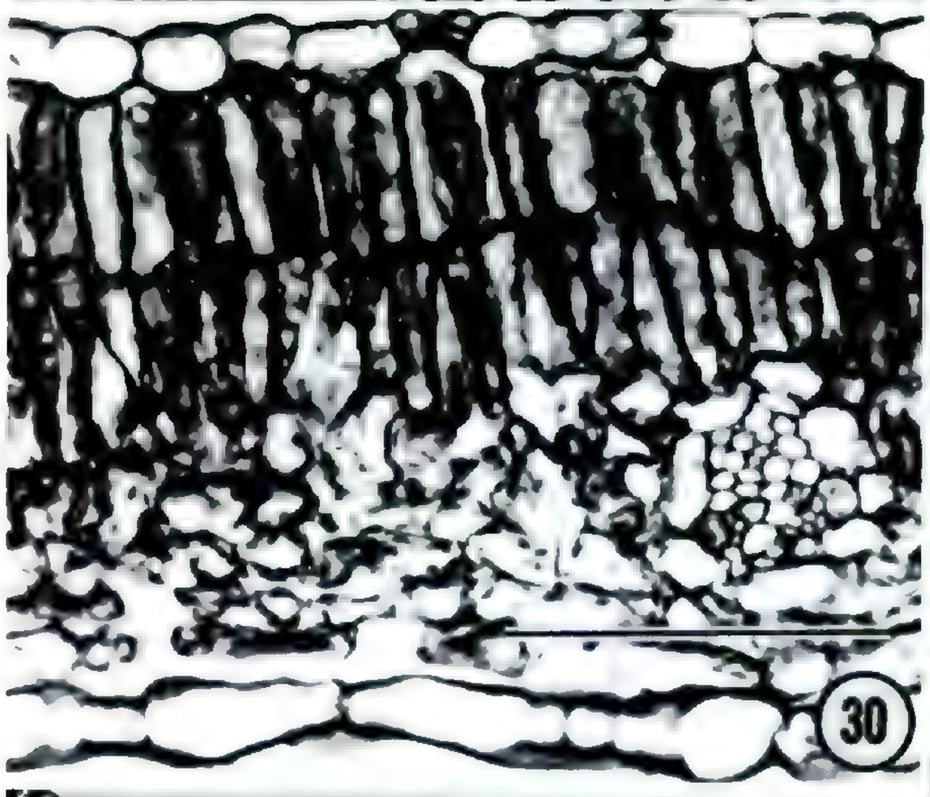
FIGURES 17–24. Leaf cross sections of Epilobieae.—17. *Epilobium suffruticosum*, midrib with broad arc midvein.—18. *E. suffruticosum*, isobilateral lamina with three palisade layers on both sides. Note the elongated vertical, thick-sheathed raphide cell.—19. *E. latifolium*, midrib with small arc midvein. Note the restricted zone of midrib ground tissue.—20. *E. pyrricolophum*, large midrib with large ground tissue area.—21. *E. dodonaei*, midrib of isobilateral leaf. Note small arc midvein surrounded by restricted ground tissue zone.—22. *E. glabellum*, broad arc midvein with no adaxial phloem.—23. *Boisduvalia macrantha*, midrib with small arc midvein.—24. *B. subulata*, midrib with small arc midvein. Raphide crystal cells (unsheathed) occur in cross section in a band in mid-mesophyll (arrows). Scale lines equal 250 μm for Figs. 17–23; 100 μm for Fig. 24.

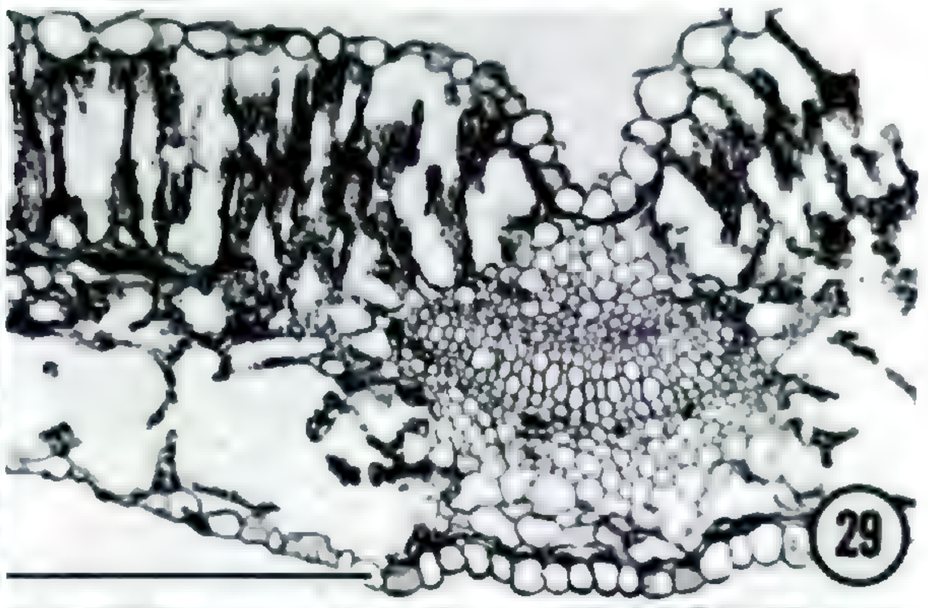


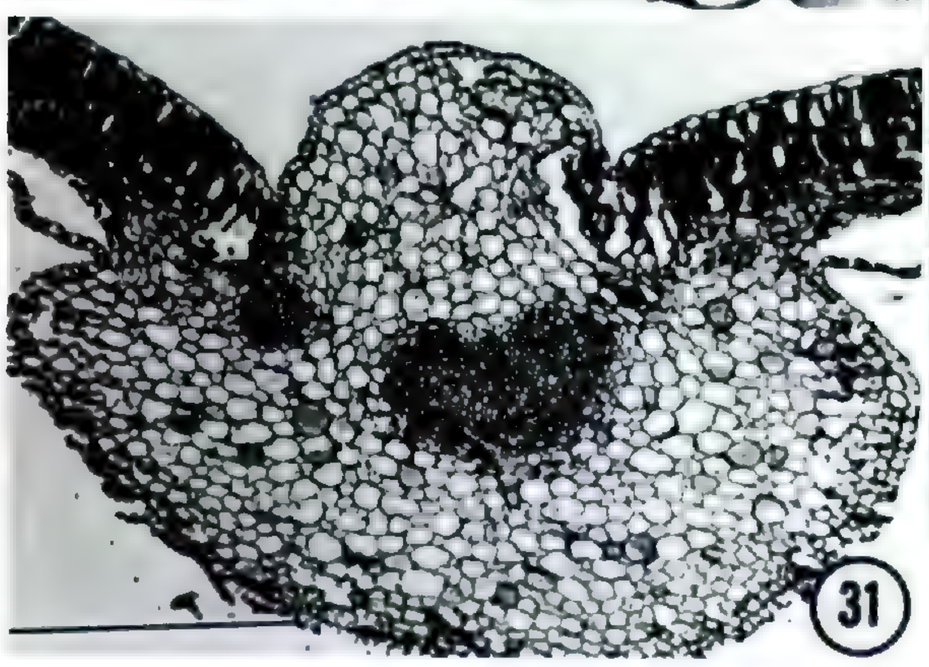


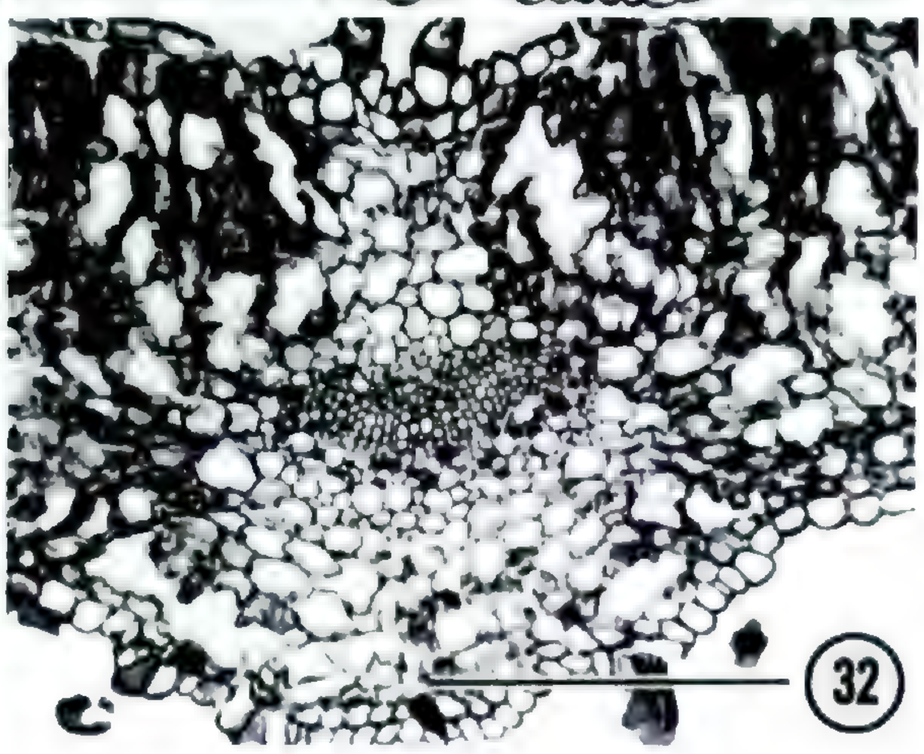




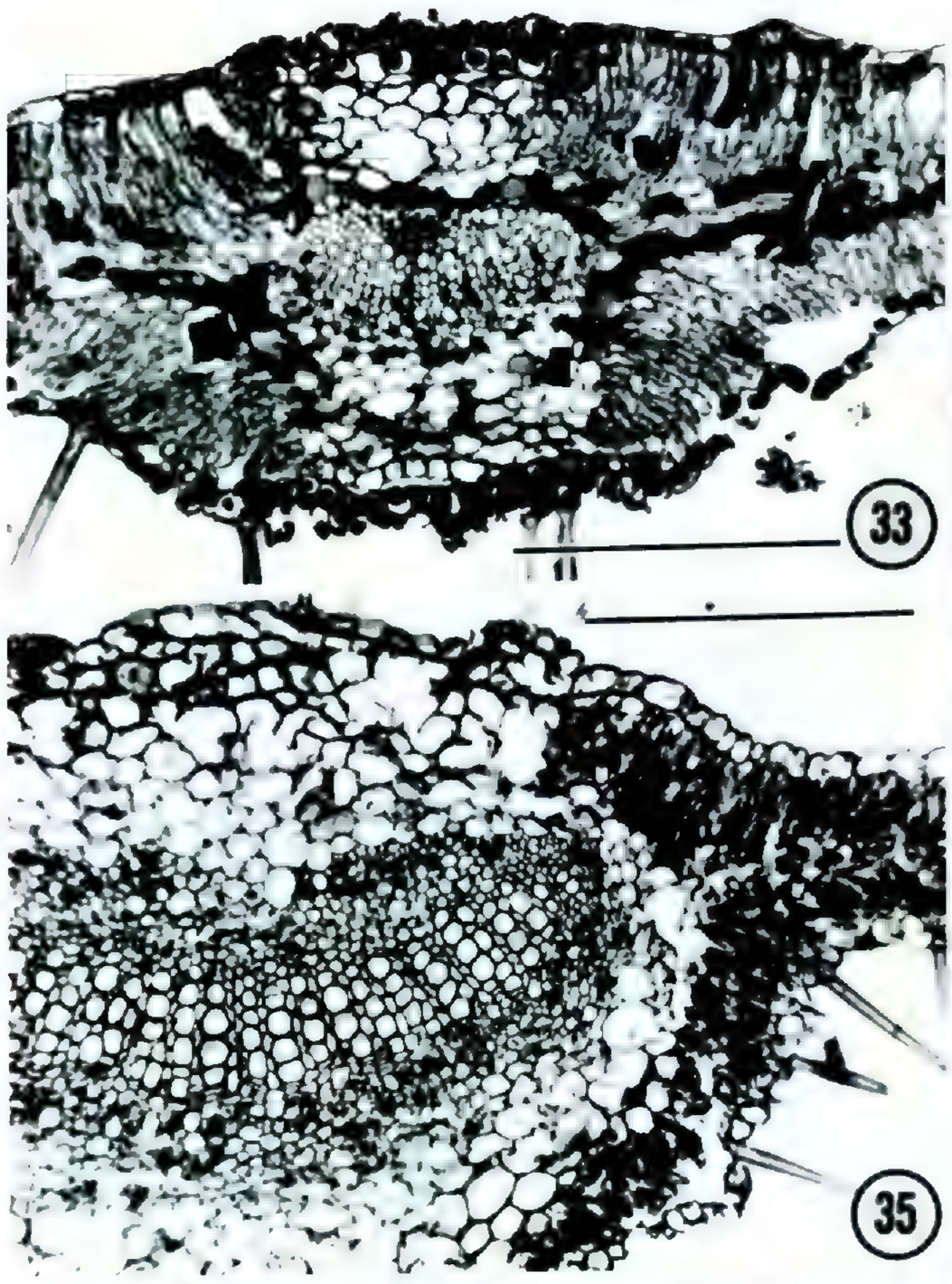


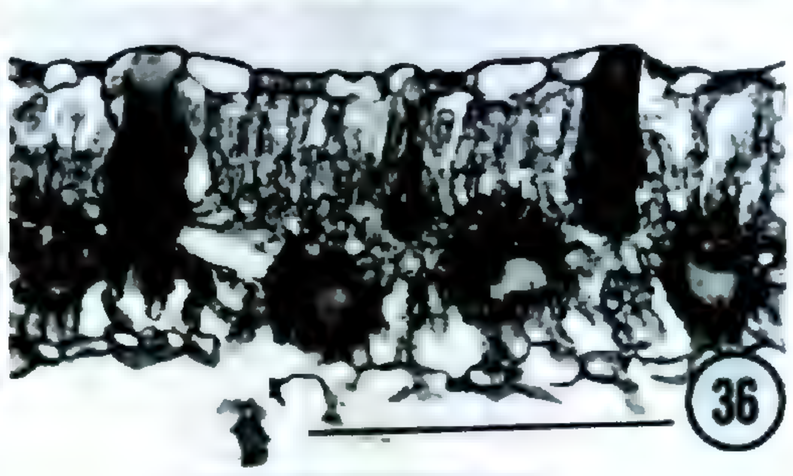


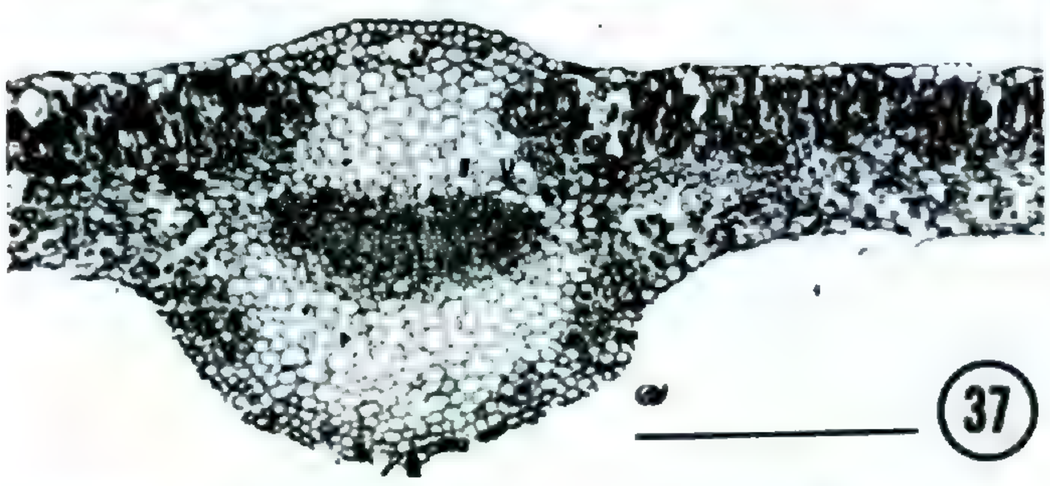


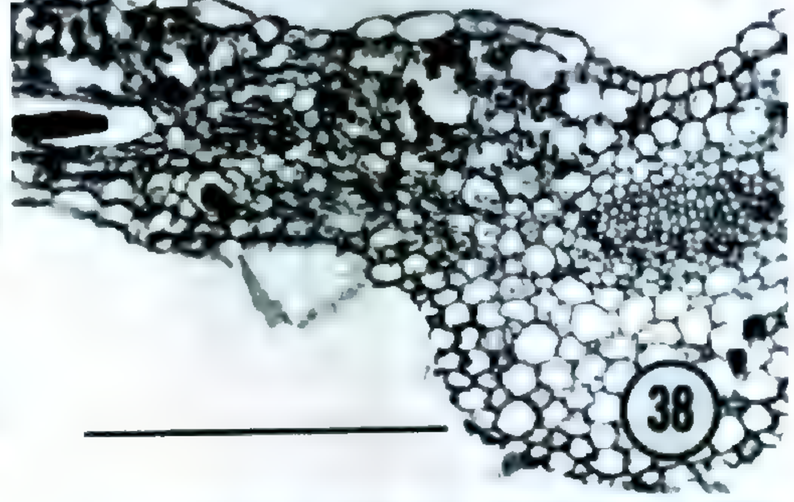


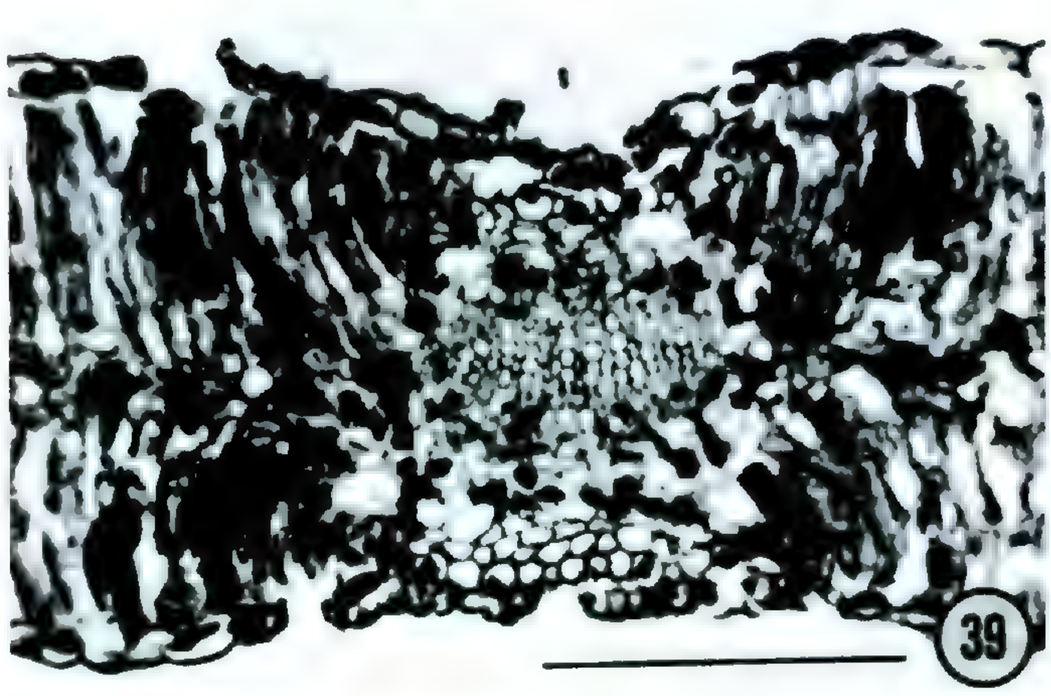
FIGURES 25–32. Leaf cross sections of group 1 Onagraeae.—25. *Gongylocarpus rubricaulis*, midrib with short arc midvein. Note poorly defined boundaries between the mesophyll and midrib ground tissue.—26. *G. rubricaulis*, lamina under polarized light showing coarse raphides.—27. *Xylonagra arborea*, midrib with abaxial and adaxial ridges.—28. *X. arborea*, lamina with adaxial stomate and a poorly differentiated mesophyll.—29. *Gayophytum heterozygum* midrib with a broad arc midvein under an adaxial groove. Midvein ground tissue does not surround the vein laterally.—30. *Camissonia ovata*, lamina with adaxial stomate and a well-differentiated lamina with two palisade layers.—31. *C. ovata*, large midrib with short arc midvein. Ground tissue zone is extensive.—32. *C. cheiranthifolia*, small midrib with a restricted midvein zone. Scale lines equal 500 μm for Fig. 31; 250 μm for Figs. 25, 27, 29, 32; 100 μm for Figs. 26, 30; 50 μm for Fig. 28.

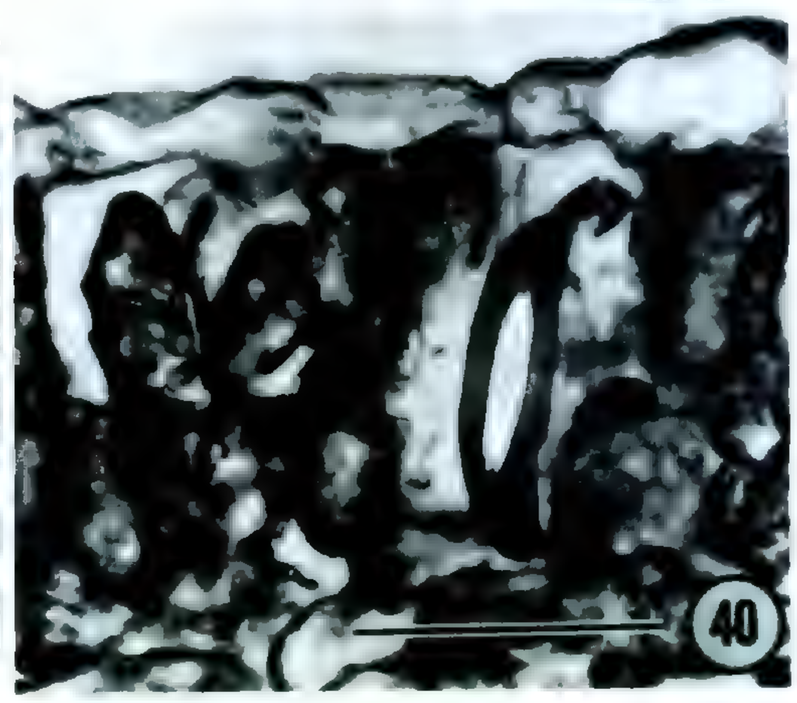




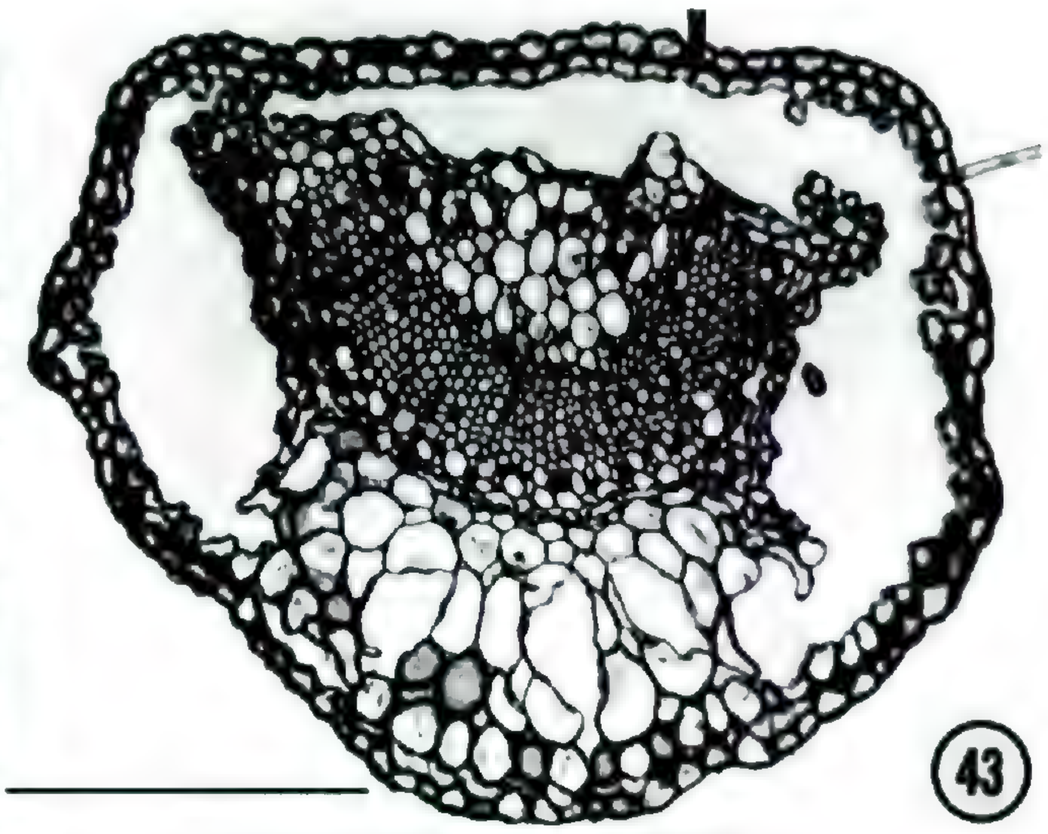


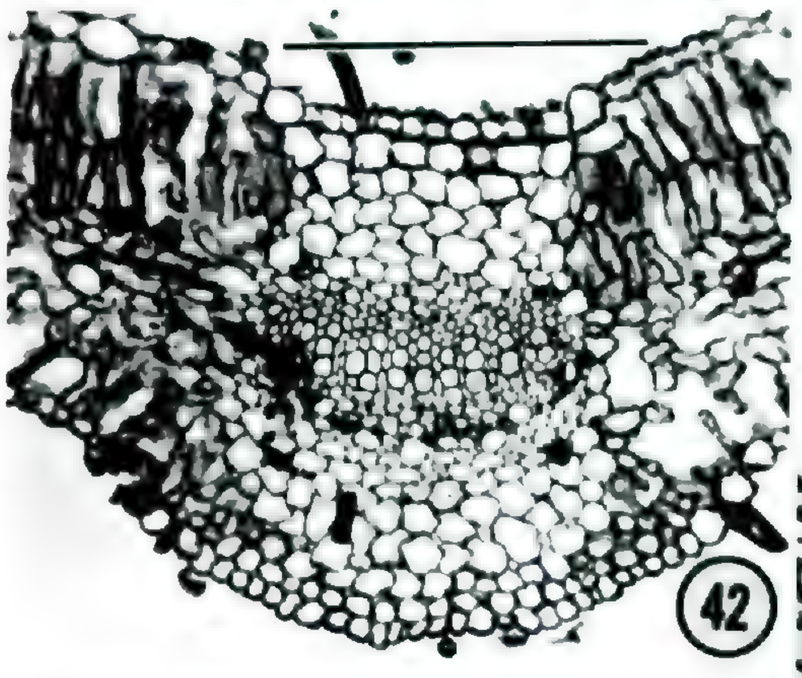


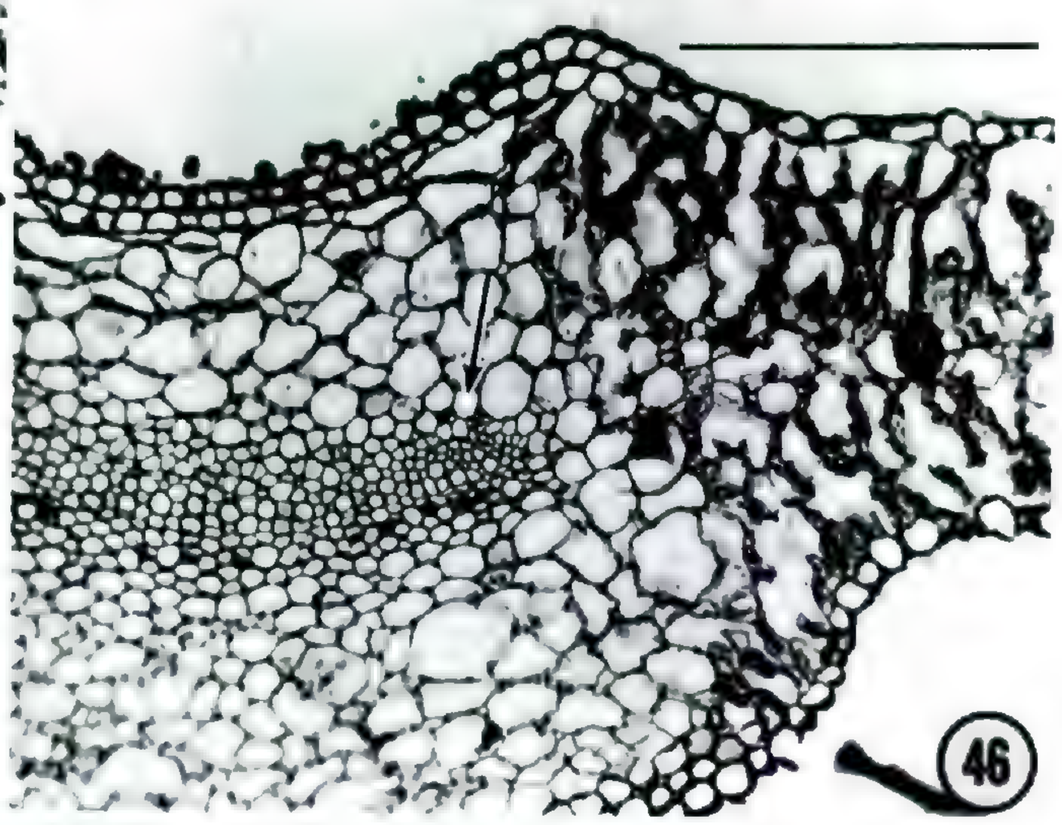


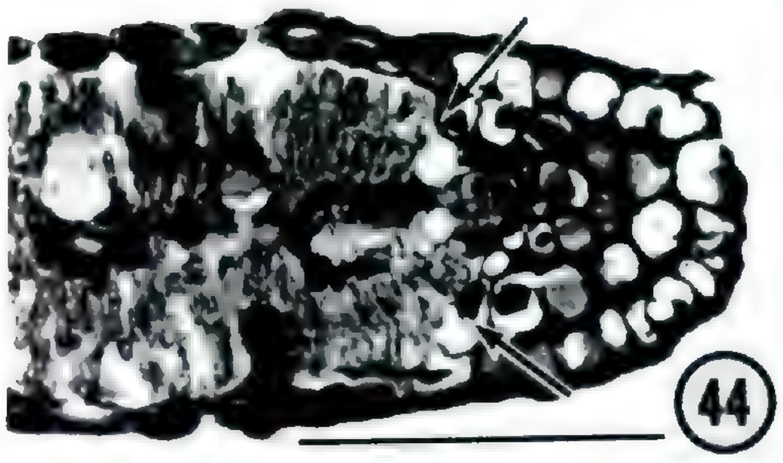


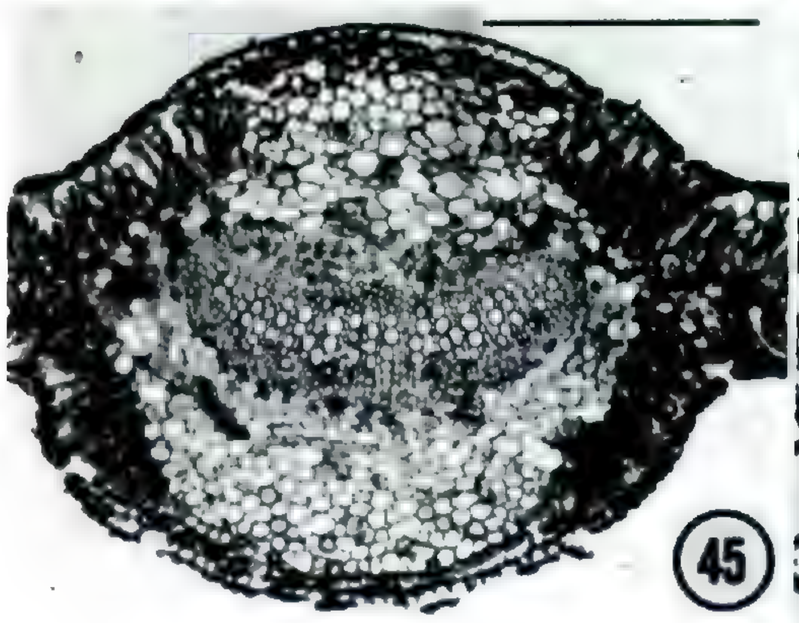
FIGURES 33–40. Leaf cross sections of group 2 Onagreae.—33. *Gaura villosa*, midrib of isobilateral leaf. The short arc midvein has ground tissue restricted to patches above and below the midvein. Note centric orientation of palisade mesophyll near the midvein.—34. *G. villosa*, lamina with stored gummy or tanniniferous materials at the epidermal layers and in mid-mesophyll. Note fine raphides in gum sheaths, horizontal at mid-mesophyll and in the palisade layer (arrows).—35. *G. parviflora*, large midrib with broad arc midvein. Note mesophyll in the midrib zone forming a concave boundary with the midrib ground tissue.—36. *G. suffulta* subsp. *suffulta*, lamina with raphides in gum sheaths oriented vertically in the palisade layer and horizontally (in cross section) in the spongy mesophyll.—37. *G. lindheimeri*, midrib with anatomy similar to Fig. 35 above but with less strongly developed mesophyll in the midrib zone.—38. *Calylophus hartwegii*, midrib and lamina. Note poorly differentiated mesophyll and indistinct boundary with the midrib ground tissue.—39. *C. berlandieri*, midrib in isobilateral leaf with no surface distentions. Note centric arrangement of palisade cells near the midvein.—40. *C. berlandieri*, adaxial portion of lamina under polarized light showing raphide crystals in a thick gum sheath. Scale lines equal 500 μm for Fig. 37; 250 μm for Figs. 33, 35, 36, 38, 39; 100 μm for Fig. 34; 50 μm for Fig. 40.

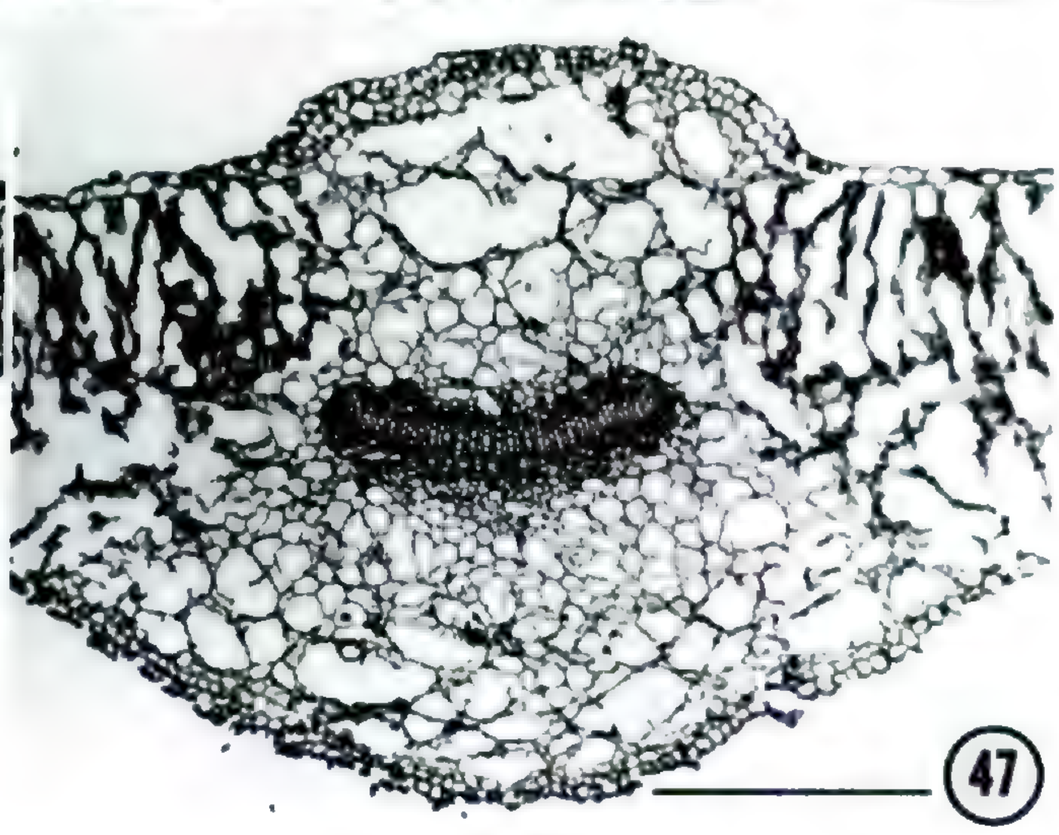




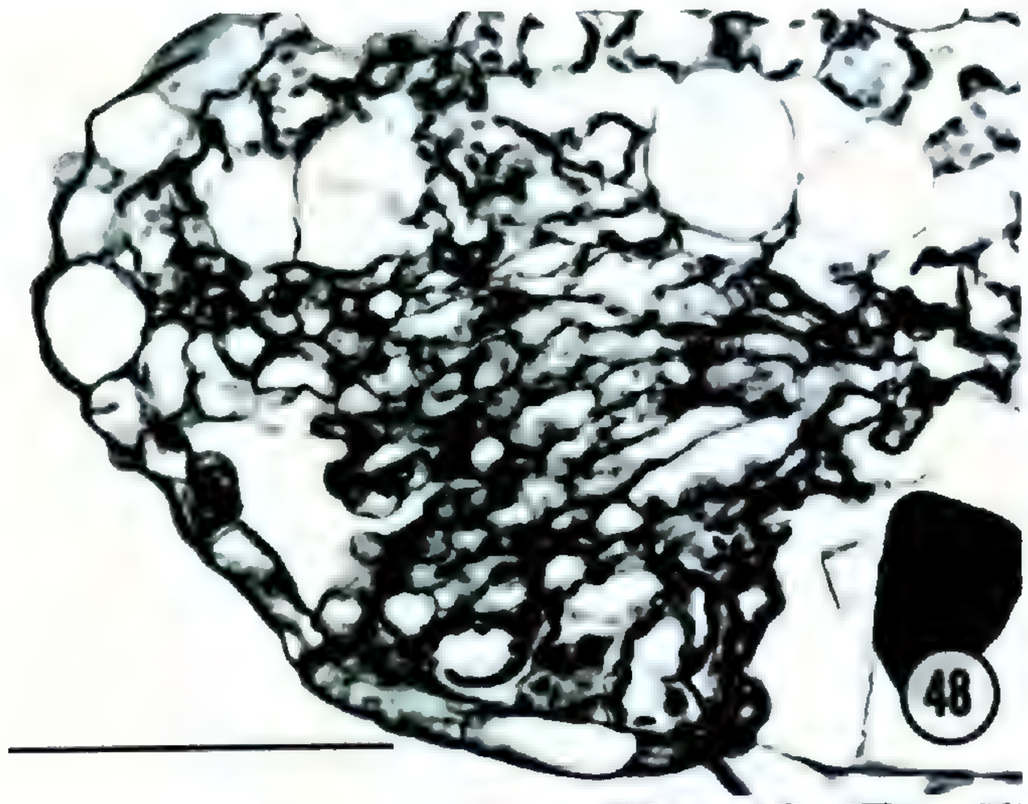


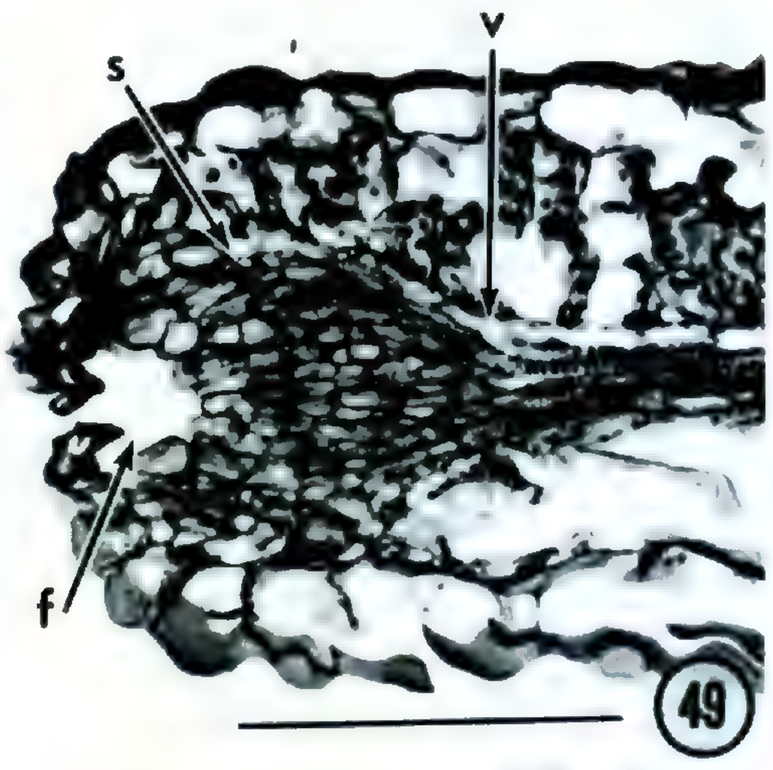


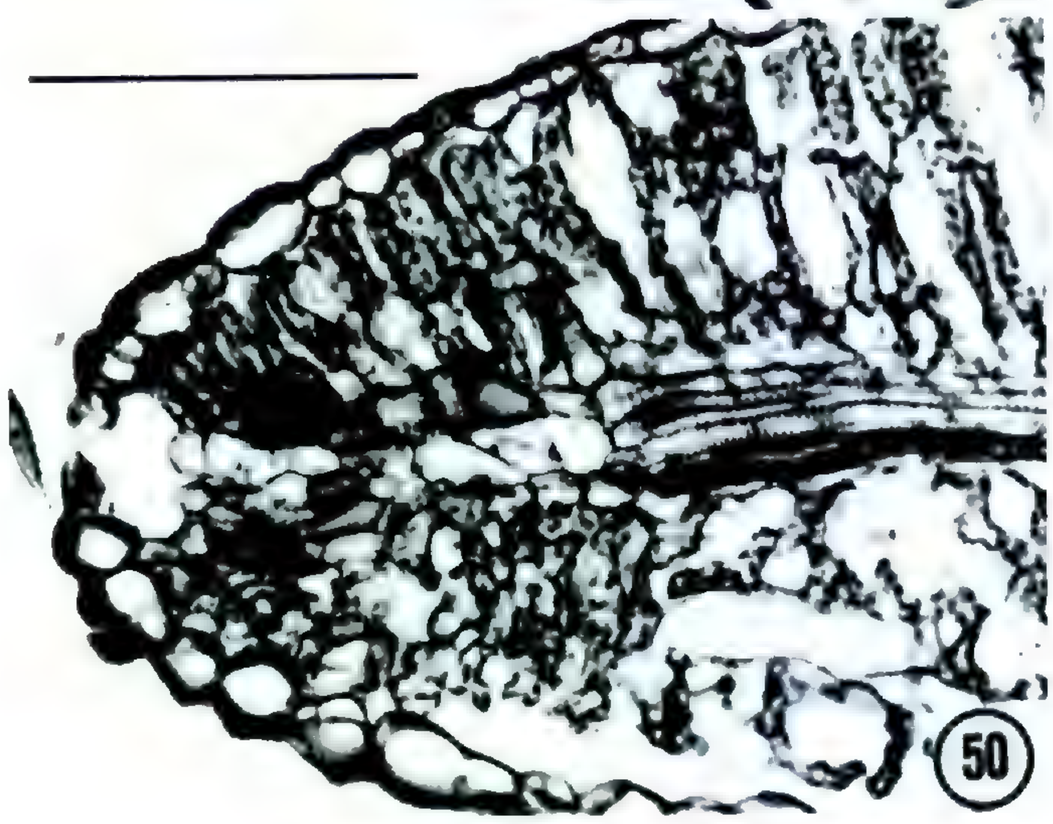


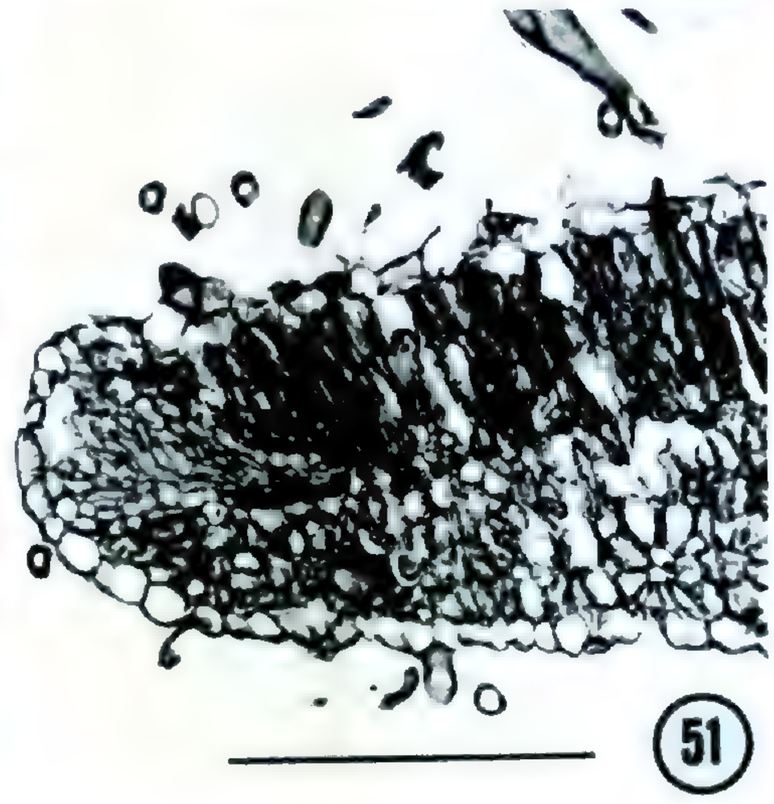


FIGURES 41–47. Leaf cross sections of groups 2 & 3 Onagreae.—41. *Clarkia rubicunda*, lamina and secondary vein. Leaf is isobilateral with well-differentiated palisade cells.—42. *C. rubicunda*, midrib and midvein with well-differentiated mesophyll and midvein-mesophyll boundary.—43. *Heterogaura heterandra*, petiole showing semicircular vein. Large spaces in the ground tissue were filled with mucilaginous material.—44. *Stenosiphon linifolius*, isobilateral lamina with mesophyll ending (arrows) well within the mechanically strengthened margin.—45. *S. linifolius*, midrib with broad midvein arc. Note the palisade mesophyll intrusion into the midrib making a concave boundary with the midrib ground tissue.—46. *Oenothera grandis*, midrib with broad midvein and limited adaxial phloem (arrow). Note pronounced adaxial midrib groove bounded by a ridge.—47. *O. macrosceles*, large midrib with broad arc midvein. Scale lines equal 500 μm for Figs. 45, 47; 250 μm for Figs. 41–44, 46.









FIGURES 48–51. Leaf cross sections showing marginal hydothodal tooth glands.—48. *Lopezia nuevo-leonis*.—49. *Epilobium melanocaulon*.—50. *Camissonia claviformis*.—51. *C. cheiranthifolia*. In all figs., note stomatal opening to the subepidermal foramen (f-arrow). Vein ending (v-arrow) expands into secretory tissue (s-arrow). Scale lines equal 250 μm for Fig. 51; 100 μm for Figs. 48–50.

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THE SYSTEMATICS AND EVOLUTION OF *CIRCAEA* (ONAGRACEAE)[1]

DAVID E. BOUFFORD[2]

ABSTRACT

Circaea (Onagraceae) is a well delimited genus and the sole member of the tribe Circaeeae. Unlike other Onagraceae, *Circaea* is restricted to the mixed mesophytic and boreal forests of the northern hemisphere and reaches its greatest diversity in eastern Asia, where 12 of the 14 taxa occur. The very closely related *C. lutetiana* subspp. *canadensis* and *quadrisulcata* exhibit the frequent pattern of disjunction between eastern North America and eastern Asia. Hybridization in the genus is common and widespread and has long been recognized in Europe and North America. In Asia, hybridization is equally widespread and more complex because of the greater number of species involved. In all cases, hybrids are highly sterile and, in crosses involving *C. alpina*, they are often completely sterile. Very little or no backcrossing and introgression occur in *Circaea*. Hybrids often form large colonies and reproduce vigorously by vegetative means. They often behave as fertile species in the genus in being wide-ranging, in occupying habitats distinct from those of the parents, in being morphologically similar from population to population and in often occupying ranges partially outside the range of one or both parents. All species are diploid with $n = 11$, the original basic chromosome number for the family. The structure of the nectaries, the leaves, and the retention of the basic chromosome number, $n = 11$, are generalized characters shared with *Fuchsia*, which is one of the most primitive genera of Onagraceae. *Fuchsia* is bird-pollinated and primarily tropical in distribution while *Circaea*, whose epizoochoric fruits are known from the Oligocene, is pollinated chiefly by syrphid flies and small bees and is temperate in distribution. It is likely that both genera were derived from a common ancestor. The ancestor of *Circaea* apparently reached North America from the probable place of origin for the family in South America. The high diversity of taxa, including the most primitive in the genus, in eastern Asia seems to be related to the favorable climatic conditions prevailing there since *Circaea* reached this region, a well-known center of survival for many Arcto-Tertiary genera, and not to an Asian origin for *Circaea*. The genus has evolved in two directions since its origin: 1) towards more efficient outcrossing through modification of the nectary so that it is more conveniently positioned for visits by short-tongued insects, primarily syrphid flies, and 2) towards self-pollination by having the anthers appressed to the stigma and dehiscing before opening of the buds, and in reduction of the locules in the ovaries and fruits from two to one. *Circaea repens* of the Himalayan region occupies an intermediate position between the two groups in the presence of a trace of a second locule. *Circaea* is treated in accordance with other recent work in the Onagraceae. Seven species are recognized. *Circaea alpina*, the most wide-ranging of the species, comprises six subspecies, each occupying a distinct ecological and/or geographical area. *Circaea lutetiana* includes three subspecies, one each in Asia, Europe, and North America. The remaining species are *C. cordata*, *C. erubescens*, *C. glabrescens*, *C. mollis*, and *C. repens*, all confined to Asia. Three new hybrids, *C.* × *skvortsovii*, *C.* × *decipiens*, and *C.* × *mentiens*, are described, one new combination, *C.* × *ovata*, is made, and two taxa are changed in status. Full descriptions are provided for the eight known hybrids in addition to those for the species and subspecies.

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INTRODUCTION

Circaea (Onagraceae) is a well-delimited genus and the sole member of the tribe Circaeeae. Unlike other Onagraceae, *Circaea* is restricted to the mixed mesophytic and boreal forests of the Northern Hemisphere and reaches its greatest diversity in eastern Asia, where 11 of the 14 taxa occur. The very closely

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related *Circaea lutetiana* subspp. *canadensis* and *quadrisulcata* exhibit the frequent pattern of disjunction between eastern North America and eastern Asia (Fernald, 1915; Hara, 1939, 1952).

Hybridization in the genus is common and widespread and has long been recognized in Europe and in North America (Ascherson & Magnus, 1870; Fernald, 1917; Hara, 1959; Cooperrider, 1962; Raven, 1963; Haber, 1967, 1977), although at times it has led to confusion or incorrect interpretation (Ehrhart, 1789; Léveillé, 1898, 1900, 1912; Fernald, 1917). Hybridization in Asia is equally widespread and was first suggested by Handel-Mazzetti (1933) and elaborated on by Hara (1936, 1959). I recently reviewed the occurrence of the genus and its hybrids in Japan (Boufford, 1982). In all cases hybrids are highly sterile and, in crosses between the most distantly related species, often completely sterile. Very little or no backcrossing and introgression occur in *Circaea* and hybrids are morphologically intermediate between the parents. Hybrids often form large colonies in naturally disturbed habitats and reproduce vigorously by vegetative means. They often occupy habitats distinct from those of the parents, are wide-ranging and morphologically similar from population to population, and often occur partially outside of the range of one or both parents (Fernald, 1917; Raven, 1963).

Circaea differs from most other Onagraceae in containing only flavones (Boufford et al., 1978; John Averett, pers. comm.). All species are diploid, with $n = 11$, the original basic chromosome number for Onagraceae, although triploids have been found in *C.* × *intermedia* (Seavey & Boufford, 1983). Pairing of the chromosomes is usually normal at meiosis, although in some combinations a ring of four chromosomes is formed, indicating the presence of reciprocal translocations differentiating some species (Seavey & Boufford, 1983).

The similarities in the leaves, in the retention of the original basic chromosome number, $n = 11$, and in the structure of the nectaries are generalized features retained both by *Circaea* and by *Fuchsia*, one of the more primitive genera of Onagraceae (Eyde & Morgan, 1973). *Fuchsia* is bird-pollinated, primarily tropical in distribution, and has fleshy fruits; whereas *Circaea*, whose epizoochoric fruits, unique in the Onagraceae, are known from the Oligocene (Dorofeev, 1963, 1969; Nikitin, 1957; Szafer, 1947), is pollinated chiefly by syrphid flies and small bees and is primarily temperate in distribution. The floral similarities between *Circaea* and *Lopezia* are only superficial, although both may have had a common ancestor with *Fuchsia*. The differences between *Circaea* and *Lopezia* have been pointed out clearly by Eyde and Morgan (1973).

The ancestor of *Circaea* apparently reached North America in Paleogene time from the probable place of origin for the family in South America. The high diversity of taxa, including the most primitive in the genus, in eastern Asia seems to be related to the favorable climatic conditions prevailing there since *Circaea* reached this region, a well known center of survival for many Arcto-Tertiary genera, rather than to an Asian origin for *Circaea*.

Circaea has evolved in two directions since its origin: 1) towards more efficient outcrossing through modification of the nectary so that it is more conveniently positioned for visitation by short-tongued insects, primarily syrphid flies, and 2) towards self-pollination by having the anthers appressed to the stigma and de-

hiscing before opening of the buds and in the reduction of the locules in the ovaries and fruits from two to one. The unilocular *Circaea repens* of the Himalayan region occupies an intermediate position between the two groups in the presence of a trace of a second locule, visible as a darkened line in freehand sections of the fruits, and in appearing to be outcrossing although otherwise resembling *C. alpina*.

Circaea is here treated in accordance with other recent work in Onagraceae (e.g., Lewis & Lewis, 1955; Plitmann et al., 1973). My treatment is based on extensive field observations in eastern North America, Japan, central China, and Taiwan, and on living plants in cultivation at Missouri Botanical Garden. Over 25,000 herbarium specimens, from throughout the entire range of the genus, were also examined. Seven species are recognized. *Circaea alpina*, the most wide-ranging species, comprises six subspecies. *Circaea lutetiana* contains three subspecies in as many geographical regions of the world. The remaining species, *C. cordata*, *C. glabrescens*, *C. mollis*, *C. erubescens*, and *C. repens*, are all confined to Asia. Full descriptions are provided for the nine known hybrids in addition to those for the species and subspecies. Three new hybrids, *C.* × *skvortsovii* (*C. cordata* × *C. lutetiana* subsp. *quadrisulcata*), *C.* × *mentiens* (*C. alpina* subsp. *alpina* × *C. erubescens*), and *C.* × *decipiens* (*C. erubescens* × *C. lutetiana* subsp. *quadrisulcata*) are named; three taxa are changed in status.

Ecology

Species of *Circaea* grow from warm-temperate, deciduous to cold, boreal forests throughout the northern hemisphere wherever sufficient year-round moisture is available. Although all species, with the possible exception of *C. alpina*, appear to have very broad ecological tolerances, familiarity with the plants in the field shows that each species grows best under fairly specific conditions.

Circaea mollis prefers the wettest conditions, often growing in standing or slow-moving water at the edge of streams and in slow seepages in thickets or open forests, usually in loamy soils. *Circaea mollis* is often abundant in *Cryptomeria* plantations along rivers throughout Japan. *Circaea erubescens* grows along cool, clear streams but in coarse sandy soils and where the water is constantly, but not rapidly, moving, and is also common in drier areas such as along forest paths, on roadside banks, and in roadside thickets.

All three subspecies of *Circaea lutetiana* are found most commonly in well drained, deep alluvial loamy soils at the upper part of flood plains or on alluvial slopes and terraces, but very rarely in flood plain depressions.

Circaea cordata prefers the most xeric conditions of any *Circaea*, being found on dry, rocky slopes or on raised ground in alluvial forests. *Circaea cordata* may also have a preference for calcareous or other basic soils. It is often found growing near conglomerate rocks or limestone.

The subspecies of *Circaea alpina*, when growing sympatrically, are for the most part separated ecologically, yet several subspecies which are geographically isolated grow in similar habitats. *Circaea alpina* subspp. *alpina*, *micrantha*, and *pacifica* grow along streams or seepages, often on moss-covered rocks and logs

or in wet siliceous soils in conifer forests at medium to high latitudes and altitudes. These three subspecies occupy different geographical areas and only *C. alpina* subspp. *alpina* and *pacifica* overlap in part of their ranges and apparently intergrade completely. *Circaea alpina* subsp. *caulescens* occurs almost totally within the range of subsp. *alpina* but prefers deeper, drier, fine-grained soils in warmer sites in the transitional zone between the mixed deciduous and boreal forests in Japan. Skvortsov (1970a, 1979) reported similar findings for the two subspecies on the Asian mainland. *Circaea alpina* subsp. *imaicola* is geographically isolated from subsp. *caulescens* but grows in similar habitats in the Himalayas, the higher mountains of southern China, and in Taiwan. *Circaea alpina* subsp. *imaicola* also grows at higher elevations in conifer forests, on slopes in seepages, and in thickets. *Circaea alpina* subsp. *imaicola* has been collected as an epiphyte in the Himalayas, and *C. alpina* subsp. *caulescens* grows as an epiphyte near Tomakomai in southern Hokkaido. The few collections of *C. alpina* subsp. *angustifolia* with ecological data indicate that this subspecies prefers warmer sites than *C. alpina* subsp. *imaicola* and grows at lower elevations where the two overlap in range. I saw this subspecies near Kunming, Yunnan, where it occurs in broad-leaved evergreen fagaceous forests. *Circaea alpina* subsp. *angustifolia* grows in fairly deep soils. Subspecies of *C. alpina* with pubescent stems grow in deeper soils in warmer habitats than do subspecies with glabrous stems, which occur in moist, cool habitats, commonly in moss.

In the mountainous regions of western Hubei, China, *Circaea glabrescens* grows in moist to dry, deep soils, usually in openings or at the margins of mixed deciduous forests. The range of *C. glabrescens* on the Chinese mainland is in a region where rainfall averages 750–1,000 mm/year (Hsieh, 1973) and it may be that this species is similar to *C. cordata* in its preference for drier conditions. However, the single collection of *C. glabrescens* from Taiwan is from an area where rainfall exceeds 2,000 mm/year (Hsieh, 1973) suggesting that other factors may also be involved.

The lack of personal observations and scanty label data make it more difficult to determine the ecological preferences of *Circaea repens*. However, *C. repens* appears to prefer deep, moist soils and is often found on slopes and in thickets. Much more detailed studies will be necessary to further clarify ecological relationships of the species of *Circaea*.

CYTOLOGY

Circaea retains the original basic chromosome number for the Onagraceae, $n = 11$. According to Kurabayashi et al. (1962), the mitotic chromosomes of *Circaea* are poorly differentiated into heterochromatic and euchromatic portions and contract more or less evenly at mitosis with the heterochromatic portions remaining visible as chromocenters during interphase. The meiotic chromosomes of *Circaea*, however, are sharply differentiated in this respect and resemble those of the tribes Onagreae and Epilobiae (Seavey and Boufford, in press). This feature may well be correlated with the presence of reciprocal translocations differentiating hybrids and in some cases occurring in natural populations in all three groups.

Seavey and Boufford (in press) review the cytology of *Circaea* and report a gametic chromosome number of $n = 11$ in all taxa except *C. alpina* subsp. *micrantha*, for which no information is available. In three of the twelve collections of *C.* × *intermedia* they examined, at least some of the individuals were triploid ($2n = 3x = 33$).

North American diploid collections of *Circaea* × *intermedia*, as well as one of the five Asian collections examined, were heterozygous for a reciprocal translocation; the others were chromosomally homozygous. Hybrids between *C. cordata* and *C. erubescens*, *C. cordata* and *C. mollis*, and *C. erubescens* and *C. lutetiana* were likewise heterozygous for a single reciprocal translocation, whereas *C. alpina* × *C. erubescens* was structurally homozygous. The simplest interpretation of these results, although not necessarily the correct one, would be that *C. alpina*, *C. erubescens*, and *C. mollis* have the same chromosome arrangement and differ by one relatively small reciprocal translocation from *C. lutetiana* and *C. cordata* (Seavey & Boufford, in press).

Reproductive Biology

The species of *Circaea* can be divided into two groups based on their mode of reproduction. All species with bilocular fruits, and probably also *C. repens*, are predominantly outcrossing but facultatively self-pollinating. *Circaea alpina*, with the possible exceptions of subsp. *caulescens* and some populations of subsp. *angustifolia*, are self-pollinating but facultatively outcrossing. All species of *Circaea*, therefore, are genetically self-compatible.

In species with bilocular, 2-seeded fruits, the flowers open around sunrise and the stigma becomes papillose and receptive a short time after anthesis. The stamens are spreading and held away from the stigma. In most species the stamens are shorter than the style so that automatic self-pollination is impossible. One anther dehisces shortly after anthesis while the other dehisces several hours later, and as late as mid-afternoon. All species, including the unilocular *Circaea alpina*, produce a small droplet of nectar from a ring-shaped nectary that surrounds the base of the style and is exserted from the floral tube in some species. The nectar usually becomes highly concentrated through evaporation by midday, if not removed by insects, and is not evident during the afternoon. At maturity of the flowers the petals are spread widely apart in a 180° plane. The sepals are most often reflexed and, with the petals, form a convenient target for insect visitors (see Kugler, 1938, fig. 3). After a day or two the flowers begin to fade and the petals close toward each other and eventually touch (see Knuth, 1908, fig. 153, and Müller, 1883, fig. 88), the stamens projecting from the openings at the sides and the style extending through the notch at the petal apices. Ultimately the floral tube abscises from the summit of the ovary and the flower falls off. Usually one, and sometimes two, flowers in a given inflorescence open each day, but progression of anthesis is dependent on ambient temperature. I have seen as many as eleven flowers open at one time on a single inflorescence of *C. lutetiana* subsp. *canadensis*, but, on the average, a single inflorescence of that taxon usually bears about five open flowers. Contrary to the report by Haber (1977) that the pedicels of *Circaea lutetiana* subsp. *canadensis* are reflexed at anthesis, they are held

perpendicular to the axis of the raceme as in all bilocular species, and become reflexed only as the flowers begin to fade.

In *Circaea alpina* the anthers regularly dehisce in the bud while appressed to the papillose and receptive stigma. Haber (1967, 1977) and Raven (1963) reported the same findings in plants from Ontario and from the British Isles. Below an ambient temperature of about 15°C or in otherwise unfavorable weather, the buds of *C. alpina* may remain closed with effective pollination taking place. Eventually the buds drop without ever having opened and the ovaries begin to develop. I have noticed that the temperature at which the flowers of *C. alpina* begin to open coincides well with the lowest temperature at which the chief insect visitors to the flowers become active. This adaptation to a means of sexual reproduction independent of the necessity of insects but with retention of the capability for outcrossing under favorable conditions no doubt accounts for the considerable success of *C. alpina* in the cool boreal forests, where it is so widespread. In most subspecies of *C. alpina* the flowers are clustered at the apex of the raceme at anthesis and form a floral unit, in contrast to the individual more or less widely spaced flowers, each functioning as a floral unit in other species of *Circaea*.

The chief visitors to all species of *Circaea* are syrphid flies, with small halictid bees being of somewhat less importance. The mode of visitation varies between different species of syrphids but the way in which the fly eventually alights on the flower is generally the same. When visiting species of *Circaea* with spreading pedicels, syrphids usually approach the base of the raceme first, even though the raceme may be highly elongated and the flowers located near the summit of the raceme. The insect hovers briefly at each maturing ovary while ascending to those which have not yet dropped their flowers. When the fly reaches a fresh flower it hovers briefly in front of the flower and then either flies on to a different raceme or approaches the flowers and eventually alights. Occasionally, syrphid flies will alight on the lowest flowers of a raceme even though these older flowers no longer produce nectar and the anthers have long since shed their pollen.

There is no particular pattern in the manner in which the fly alights on the flower and the insect may grasp any convenient floral part in doing so. Very rarely do the flies approach directly from the front of the flower and grasp the stamens and style in the manner described by Knuth (1908) and Haber (1977). After alighting, the fly maneuvers into various positions while licking nectar from the summit of the floral tube. This constant maneuvering for position while working around the base of the style brings the insect's body in contact with both anthers and stigma. In all species of *Circaea*, several flowers on each raceme are open at the same time and the fly may visit several flowers on the same raceme or fly on to a different plant after visiting only a single flower. When visiting the flowers of *Circaea cordata*, which has closely spaced flowers at the summit of the raceme, syrphids usually walk from flower to flower. On other species with spreading pedicels which are more distantly spaced, syrphids fly from one flower to another.

All subpsecies of *Circaea alpina*, with the exception of subspp. *angustifolia* and *caulescens*, have flowers that are borne in dense corymbiform clusters on erect or ascending pedicels and the manner in which syrphids approach these flowers is different from the way they approach flowers on spreading pedicels.

Instead of flying to the base of the raceme, flies approach directly from the top of the cluster of flowers. Flies usually probe each flower for the tiny amount of available nectar and in so doing they come in contact with all open flowers as they walk around the inflorescence from flower to flower.

It is interesting that when syrphids are visiting flowers in a mixed population of plants with both widely spaced and corymbiform flowers, they need from one to three visits to a particular species before they become reoriented to that type of inflorescence. In other words, after visiting several plants with spreading pedicels and approaching from the base or middle of the raceme, a fly will continue to approach from the base or middle of the raceme after switching over to a plant with a corymbiform inflorescence. After visiting one to three consecutive plants with corymbiform inflorescences a fly will then "learn" to approach this type of inflorescence from the top rather than from below.

In mid- to late afternoon some syrphids lick the anthers and stigma in addition to the base of the style or disc, apparently in search of pollen. Halictid bees usually collect only pollen but occasionally appear to be taking nectar also. The insect makes contact with the anthers and stigma in all of the above cases. Differences in the ratios of syrphid flies to halictid bees in different habitats on the flowers of bilocular species of *Circaea* in North America and in Japan agree well with the findings of Kugler (1938) in Europe. Kugler found that in moist habitats *C. lutetiana* subsp. *lutetiana* is visited mostly by syrphid flies while on drier, upland sites halictid bees become more important.

The small halictid bees differ from syrphids in being more deliberate and systematic visitors to *Circaea* flowers and in seeking primarily pollen rather than nectar. Halictid bees also tend to replace syrphids in portions of *Circaea* populations that are in bright sunlight. Bees usually visit all flowers of one inflorescence before moving to a different inflorescence. Instead of hovering in front of each flower before alighting, as do most syrphids, halictids usually fly directly to an open flower and alight, most often grasping some part of the corolla in doing so. The bee then maneuvers for position so that it can grasp a filament with its forelegs, then bends it so that pollen can be easily taken from the anthers. The constant maneuvering brings the bee into frequent contact with the stigma. Occasionally bees were observed licking the portion of the flower near the opening of the floral tube, presumably in search of nectar.

The single most common syrphid on *Circaea* in eastern North America is *Toxomerus geminatus* (Say) with *Melanostoma mellinum* (Linnaeus), *Meliscaeva cinctella* (Zetterstedt), *Rhingia nasica* (Say), and various species of *Sphegina* being of somewhat lesser importance. In Japan, *Episyrphus balteatus* (DeGeer), *Paragus haemorrhous* Meigen, *Sphaerophoria macrogaster* (Thompson) and *Baccha maculata* Walker are the most common syrphids on *Circaea*. Other species of Syrphidae are far less common visitors.

Dialictus abanaci (Crawford), *D. atlanticus* Mitchell and *D. leavissimus* (Smith) are the most common Halictidae on the flowers of *Circaea* in eastern North America. The Japanese species of Halictidae were determined by Y. Hirashima of Kyushu University, Japan, and will be reported on in a subsequent paper, along with a more detailed account of pollination in *Circaea*.

All flies collected on *Circaea* are deposited in the collection of the Insect

Identification and Beneficial Insect Introduction Institute, Beltsville, Maryland. The bees are deposited in the collections of the Department of Entomology, University of Kansas, Lawrence, Kansas, and the Department of Entomology, Cornell University, Ithaca, New York.

Other insects such as Lepidoptera, large Hymenoptera (bumblebees), ants, *Drosophila* and other small flies seem to be only casual visitors; they very rarely effect pollination in *Circaea*.

In addition to sexual reproduction, all species of *Circaea* produce underground rhizomes by which they form small to large colonies. This may be the most important means by which the species increase population size in certain habitats. All plants in a population tend to be morphologically very similar even though differences in plants from widely scattered populations are obvious. This is especially true in hybrids, which are nearly or totally sterile and which reproduce by rhizomes even more vigorously than the parents. Despite the fact that species of *Circaea* may occur in colonies of several square meters, it may be that a colony represents only a single genotype with each individual having been derived solely by vegetative reproduction.

RELATIONSHIPS OF THE TRIBE

The monogeneric Circaeeae are distinct from other tribes of Onagraceae in having 2-merous flowers, the two stamens opposite the sepals, epizoochoric fruits, and in having the viscin threads on the pollen often greatly reduced in number or absent (Skvarla et al., 1978). Unlike other Onagraceae, the center of greatest diversity in *Circaea* is in eastern Asia. Despite these distinct character states, however, attempts to place *Circaea* in a family separate from the Onagraceae (Dulac, 1867; Nieuwland, 1914) are illogical. *Circaea* is more closely related to the line of Onagraceae, containing such genera as *Oenothera*, *Gaura*, *Fuchsia*, and *Epilobium*, than is *Ludwigia*, a genus that has never been questioned as belonging to the family.

Circaea exhibits such diagnostic onagraceous features as an *Oenothera*-type embryo sac (Maheshwari, 1950), intraxylary phloem (Metcalfe & Chalk, 1950), viscin threads on the pollen (Skvarla et al., 1978), and numerous raphid crystals throughout the plant body. *Circaea* retains the original basic chromosome number for the Onagraceae, $n = 11$, and is similar to the monogeneric Fuchsieae and Lopezieae (and *Gongylocarpus* of the Onagreae) in that respect. Eyde and Morgan (1973) have shown that *Circaea* and *Lopezia* are not closely related, leaving Fuchsieae as the tribe with which Circaeeae share the greatest number of characters, although the features they have in common are all generalized ones not indicating direct relationship.

PHYLOGENETIC RELATIONSHIPS OF THE SPECIES

In determining phylogenetic trends within the genus it is obvious that *Circaea alpina*, which is primarily self-pollinating, has the number of locules reduced to one, lacks viscin threads on the pollen (unique in the family; Skvarla et al., 1978), and produces tubers at the tips of filiform rhizomes, is an advanced species that could not be considered ancestral to any of the other species. Also, since no

other Onagraceae have the nectary projecting beyond the floral tube, it seems unlikely that the primitive *Circaea* should have such a structure. Using these criteria, the primitive species should be outcrossing, have the nectary included wholly within the floral tube, produce bilocular fruits, and have rhizomes without tuberous thickenings. The only two species that fit into this category are *C. cordata* and *C. glabrescens*. The more prominent and sometimes persistent stipules, which are soon caducous in other species, and the occasional 3- or, less often, 4-merous flowers seem to indicate that *C. cordata* is the more primitive of the two. It is, of course, highly unlikely that *C. cordata*, or any other extant species, has given rise to any of the other living members.

From the ancestral species of *Circaea*, an adaptation to pollination by syrphid flies and short-tongued bees provided selection pressures that favored elongation of the nectary so that it is positioned above the opening of the floral tube and is more convenient to insect visitors in the outcrossing species. In the inbreeding *C. alpina*, such selection pressures apparently have not affected the nectary, which remains, as in the primitive species, wholly within the floral tube. This may be correlated with the fact that an insect visitor is able to obtain the minute droplets of nectar from a number of flowers in the crowded inflorescence without expending the energy to fly, as in most Asteraceae. If *C. repens* can be thought of as an intermediate stage along the way to *C. alpina*, the retention of the nectary within the floral tube is understandable.

Figure 1 illustrates the proposed phylogenetic relationships of the species of *Circaea*.

Hybridization

Interspecific hybridization in *Circaea* is extremely common and widespread and has been the source of much confusion in the genus since 1789 when Ehrhart first described *C. intermedia*. He added the comment that Linnaeus might regard it as a hybrid between *C. alpina* and *C. lutetiana*. Reasons for the confusion have resulted from the fact that hybrids may occur outside of the range of one or both parents, vegetatively they may be more similar to one parent (although analysis of flowers and other critical features reveals their intermediate nature), and they often behave like species in being wide-ranging, growing in habitats more or less distinct from those of the parents, and in occupying a generally well-defined geographical range. Vigorous vegetative reproduction in the hybrids more than makes up for their very low fertility or complete sterility. Raven (1963) clarified the situation in the British Isles where *C. alpina* subsp. *alpina*, *C. lutetiana* subsp. *lutetiana*, and their sterile hybrid, *C.* × *intermedia*, had often been somewhat confused. The results of Raven's studies are equally applicable to all of Europe, where *C.* × *intermedia* is common and widepread, and to North America and Asia where different subspecies of *C. lutetiana* are involved in the parentage of similar hybrids. Despite the fact that all three subspecies of *C. lutetiana* hybridize with *C. alpina* subsp. *alpina* to produce *C.* × *intermedia*, plants of *C.* × *intermedia* from any of the three geographical areas of the subspecies are usually morphologically indistinguishable from each other. In addition to the studies of Raven (1963) in the British Isles, the studies by Haber (1967,

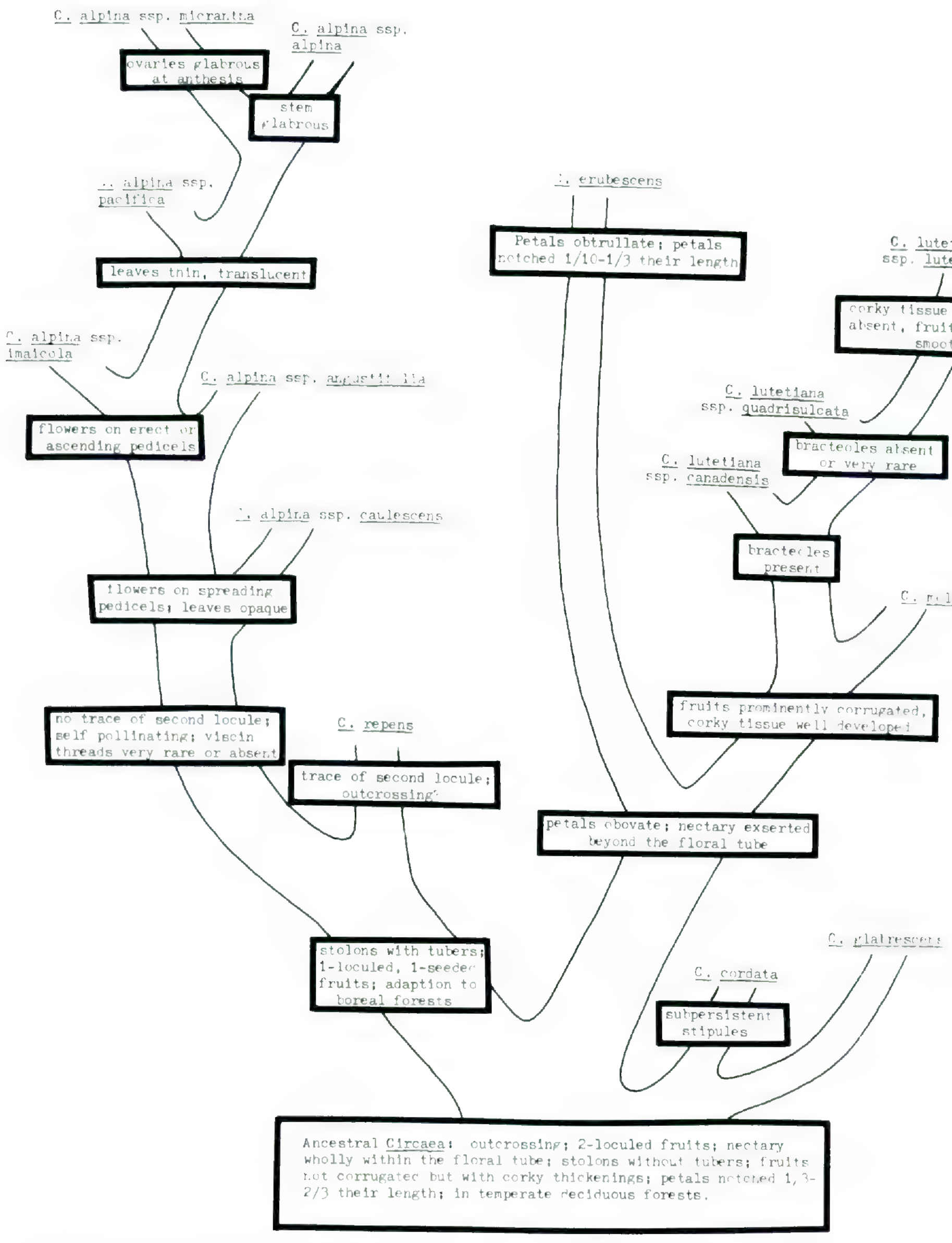


FIGURE 1. Proposed phylogenetic relationships of the species of *Circaea*.

1977) in Ontario and Cooperrider (1962) in Ohio further serve to emphasize the intermediate nature of *C.* × *intermedia* between the two parental species.

In eastern Asia hybrids are also common but much more complex due to the greater number of parental species involved and have resulted in many misidentifications and wrong interpretations. Handel-Mazzetti (1933) was the first to suggest hybridization between Asian species. He reported a hybrid between *Circaea cordata* and *C. mollis*, which he named *C.* × *hybrida*, but the type specimen of this entity (*Forrest 13254*, E) is actually a not uncommon form of *C. cordata* with

rounded to subcordate leaves. Unlike true hybrids of this parentage, the type specimen has highly fertile pollen. Hara's (1934) interpretation of the specimen collected by *Nakai, Honda & Kitagawa, 27 August 1933* (TI), on which he based his *C.* × *kitagawae* as a tentative hybrid between *C. cordata* and *C. lutetiana* subsp. *quadrisulcata* is also *C. cordata,* again with rounded or subcordate leaf bases and with pubescence more sparse than in the majority of plants of *C. cordata*. Again, the type specimen is fertile, with abundant fruit set.

In 1936, Hara named *Circaea* × *dubia* and correctly interpreted it as being a hybrid between *C. cordata* and *C. erubescens*. This combination is the most frequent hybrid in *Circaea* in Japan and perhaps in all of eastern Asia. Later, Hara (1959), in a more elaborate account of hybridization in *Circaea,* was the first to point out the occurrence of hybrids between *Circaea alpina* subsp. *alpina* and *C. lutetiana* subsp. *quadrisulcata* in Asia. However, the plants that Hara called *C.* × *dubia* var. *makinoi* (Japan, Mt. Takao, *Makino in 1921*; MAK; isotypes: S, TI), which he thought were forms of *C. cordata* × *C. erubescens*, are actually *C. alpina* subsp. *caulescens* and typical of that subspecies.

Plants that Honda (1932) called *Circaea quadrisulcata* var. *ovata* (*H. Sekimoto 13*; TI) are identical to hybrids of *C. cordata* × *C. mollis*. The type specimen lacks fruits and its pollen was presumably sterile. Hara (1936) first considered these plants to be a variety of *C. quadrisulcata*; he later (1959) thought that they might be *C. erubescens* × *C. mollis* but failed to make the appropriate new combination. These plants are here treated as *C.* × *ovata*. I studied plants identical to *C.* × *ovata* growing in a *Cryptomeria* plantation with a mixed population of *C. cordata* and *C. mollis* at the northwest base of Mt. Maru-yama in Sapporo, Hokkaido (*Boufford & Wood 19855,* KYO, MO).

Skvortsov (1977), in an account of *Circaea* for the eastern U.S.S.R., reported *C.* × *intermedia* (*C. alpina* subsp. *alpina* × *C. lutetiana* subsp. *quadrisulcata*) from the Far Eastern part of the Soviet Union where it is rare. He showed that plants from the Soviet Far East that had been called *C. erubescens* are, in fact, this hybrid.

Several other hybrids that are apparently less common also occur naturally. These are discussed individually following the treatment of the species in the systematic section. In addition to these, two specimens (Japan, Miyagi Prefecture (Rikuzen), Narugo, Kawatabi, *K. Sugawara in 1965* (MO) and China, SW Hebei, *Y. Liu 13458* (PE) representing possible hybrids between *Circaea alpina* subsp. *alpina* and *C. cordata* have also been studied. In habit, these plants resemble *C. cordata* but are almost totally glabrous. The nectary is wholly within the floral tube and the lower leaves have rather sharp but low teeth. The leaf bases are rounded rather than cordate in the specimen from Japan, however, and would not be expected in a hybrid of this combination. Insufficient buds are available for pollen analysis to determine fertility. These sites should be revisited in an attempt to obtain more material and to observe the plants in the field in order to determine their parentage. Hybrids between *C. alpina* and *C. cordata* are certainly to be expected. *Circaea alpina* subsp. *alpina* and *C. cordata* grow within a few meters of each other on Rishiri Island in Japan and doubtless also in close contact elsewhere.

Hybrids in *Circaea* are perhaps more common than collections indicate. Some

colonies of hybrids remain totally vegetative or produce only a few, often markedly reduced, inflorescences. These plants are probably passed over by collectors as sterile plants of one of the species. Known hybrids involving *C. alpina* and any of the species with bilocular fruits are especially prone to this behavior, which probably reflects their relatively distant relationship. However, in some hybrid populations (e.g., *C. alpina* subsp. *alpina* × *C. lutetiana* subsp. *canadensis* from Jefferson Co., Pennsylvania, *Boufford 18829*, KYO, MO), flowering is especially prolific. This may be more apparent than real for it may be that unfertilized flowers of *Circaea* remain fresh and persist on an inflorescence for a greater period of time than flowers that are fertilized shortly after opening.

All hybrids in *Circaea* are most common in disturbed areas, and most often in those that are naturally caused. Disturbances caused by man tend to be more drastic and usually result in the destruction of the canopy under which all species of the shade-loving genus *Circaea* grow. Natural disturbances are usually related to flooding along small- to medium-sized streams, which often removes less aggressive herbaceous species from the immediate stream margins. Hybrids are also found away from stream margins in forests where the ground cover has been disturbed. Once hybrids have become established they are often very aggressive, competing favorably with other species and forming colonies of several square meters. Hybrids in *Circaea* reproduce very vigorously by rhizomes and often increase their ranges when pieces of rhizomes break off from the parent plant. Rhizomes are transported, probably most often by water, to other suitable sites. The frequent, extensive populations of morphologically identical plants, which occur along streams for several hundred meters, or even several kilometers as in the case of *C.* × *dubia* (*C. cordata* × *C. erubescens*, *Boufford & Wood 19798* and *19806*; KYO, MO) along the Okoppe-gawa River in northern Hokkaido, indicate that reproduction by rhizomes may be more common than reintroduction from seeds produced by frequent hybridizations between the parents. The absence of hybrids in mature, undisturbed forests where two or more species grow together as at Mt. Riga, Litchfield County, Connecticut (*C. lutetiana* subsp. *canadensis*, *Boufford & Ahles 18834*; *C. alpina* subsp. *alpina*, *Boufford & Ahles 18833*) and at Shibecha Experimental Forest on Hokkaido (*C. alpina* subsp. *caulescens*, *Boufford & Wood 19761*; *C. erubescens*, *Boufford & Wood 19764*; *C. lutetiana* subsp. *quadrisulcata*, *Boufford & Wood 19765*) further serves to emphasize that disturbance is necessary for the hybrids to become established.

Raven (1963) has given two possible explanations for the occurrence of hybrids outside of the range of one or both parents. One is that the hybrids have been introduced into favorable sites outside of the range of one or both parents by the transport of rhizomes. The other is that hybrids have persisted in sites where they were formed at some time in the past when climatic conditions were favorable for both parental species to grow there together. Also, in Britain, *Circaea* may be spread as a weed in garden soil. Another possibility is that fruits resulting from cross-pollination of one species of *Circaea* by another may be carried by animals, most likely birds, to favorable sites outside of the range of one or both parents. It seems most likely that all of the above processes have played some part in the present-day distribution of the hybrids.

Despite the high incidence of hybridization in *Circaea*, no evidence of back-

crossing or introgression was found either in North America or Japan. Raven (1963), however, indicated that some backcrossing between *C.* × *intermedia* and *C. lutetiana* subsp. *lutetiana* might take place in the British Isles and that plants referable to *C. lutetiana* var. *cordifolia* Lasch could have resulted from introgression. Weimarck (1973, 1974), using comparative chromatography, but without attempting identification of compounds, suggested possible introgression of *C. alpina* subsp. *alpina* into *C. lutetiana* subsp. *lutetiana* in Sweden. Benoit (1966, 1975) has synthesized *C.* × *intermedia* by applying pollen from *C. lutetiana* subsp. *lutetiana* to the stigma of *C. alpina* subsp. *alpina*. He (Benoit, 1975) has been able to obtain fruits from backcrosses using *C.* × *intermedia* as the pistillate parent and *C. lutetiana* subsp. *lutetiana* as the pollen donor, but it is not known if the resulting seeds are viable.

Hybrids of all combinations thus far examined are highly or completely sterile. Crosses involving *Circaea alpina* subsp. *alpina* and species with bilocular fruits are usually totally sterile although occasional plants may have a few filled grains, still rarely exceeding 1% of the total in a given plant. Also, interspecific hybrids involving this species frequently produce many 2-, 4-, and 5-pored pollen in addition to normal 3-pored grains. Percent fertility, based on the number of good pollen grains determined by the method described by Alexander (1969) or with cotton blue in lactophenol, is indicated in the discussion of each of the hybrids.

Hybrids between different species of *Circaea* are most easily recognized in the field by the absence of developing fruits on the elongating raceme axes. Absence of fruits and a high degree of sterility of the pollen are almost always a clear indication of hybridization in *Circaea*. Close examination is needed to determine parentage of hybrids in Asia, especially if one or both parental species are absent from the vicinity of hybrid populations. All hybrids in *Circaea* are usually completely intermediate between the parents morphologically. Hybrids between species having an exserted nectary and those with an included nectary always have the nectary represented by a low, ring-like disc at least partially exserted beyond the opening of the floral tube. Hybrids involving *C. cordata*, which has villous hairs, always have at least a few long hairs on some part of the plant, although the long, straight hairs on the stem of *C. cordata* are usually modified to short falcate hairs on the stems in hybrids. Hybrids between species with darkened nodes and those with green nodes always have the nodes darkened but intermediate in intensity between those of the parents.

Crosses between subspecies of the same species are a completely different matter and would probably be unrecognizable as hybrids. Subspecies of the same species are similar in critical diagnostic features and differ only in pubescence, coloration of the stem, shape and dentition of the leaves, and other more subtle characters. Hybrids between subspecies of the same species would probably be interpreted as belonging to one subspecies or the other. This is especially true within *Circaea alpina*, where subspecies often exhibit morphological intergradation and overlapping ranges. Examples of plants that appear to be intermediate between the various subspecies and which possibly represent intersubspecific hybrids are discussed under the systematic treatment of *C. alpina*.

Further discussions of hybridization are given in the taxonomic treatment.

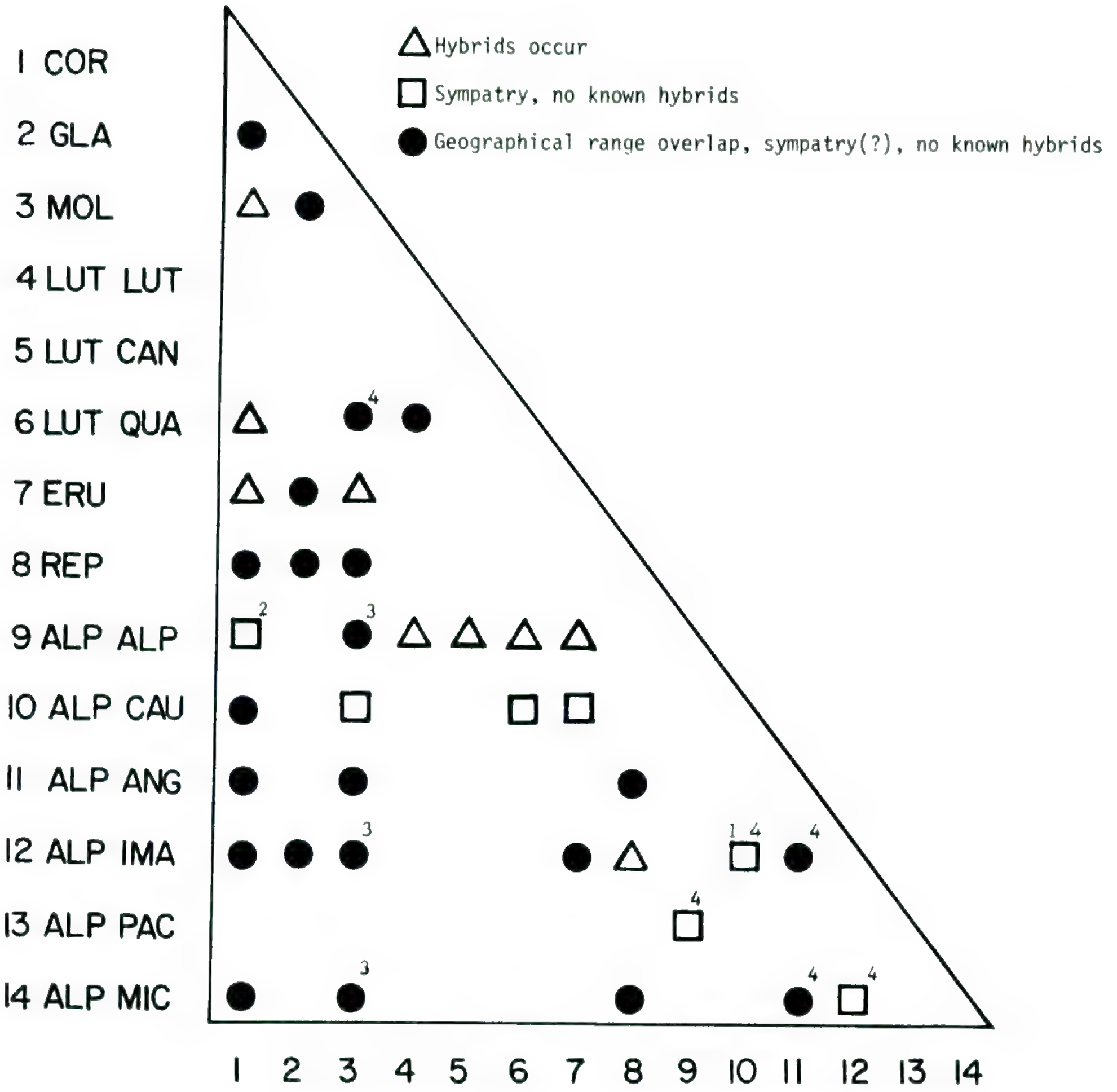


FIGURE 2. Hybridization, sympatry, and geographical range overlap in *Circaea*.—1. *Circaea alpina* subspp. *caulescens* and *imaicola* occur together in China, Anhui Province, on Mt. Huang Shan.—2. *K. Sugawara s.n.* (MO) from Japan, Miyagi Prefecture (Rikuzen Province), Narugo, Kawatabi, and *Y. Liu 13458* (PE) from China, SW Hebei, appear to be hybrids between *Circaea alpina* subsp. *alpina* and *C. cordata*.—3. Probably separated altitudinally.—4. Hybrids which, if they occur, would probably be unrecognizable as such.

Names are provided for hybrids where sufficient material exists to conclusively determine parentage. I have not been able to examine the hybrids between *Circaea alpina* subsp. *imaicola* and *C. repens* nor those between *C. erubescens* and *C. mollis* in the field. The few specimens that exist are insufficient and it therefore seems unwise to apply names to those hybrids at the present time. Further field work is necessary to resolve these two putative hybrids.

Figure 2 illustrates the sympatric occurrence and known instances of hybridization in nature for all taxa of *Circaea*. While it is highly likely that all possible combinations of hybrids can be produced, in several cases the hybrids would probably not be distinguishable from one of the parents, especially in

closely related taxa where pollen fertility might be quite high. Sympatry is here used in a broad sense, meaning only that the ranges of the taxa overlap. Where it is known for certain, either through observations or through mixed collections on herbarium sheets, that the taxa actually grow side by side, this is so indicated.

Taxonomic History

The name *Circaea* can be traced back to Dioscorides who originally used it as the name for *Mandragora officinalis* (probably the source of the common names Hexenkraut and Enchanter's Nightshade); it was later transferred to the present genus by Matthioli (Hegi, 1925). Linnaeus (1753), in *Species Plantarum*, provided descriptions for *C. alpina* and *C. lutetiana*, both of which he knew well, and for *C. lutetiana β canadensis*, whose description he adopted from Tournefort for the plants from North America. Ehrhart (1789), in naming *C. intermedia*, was the first to suggest hybridization in *Circaea*, even though he considered the plants he was naming to be a species, by adding the comment to his original description that Linnaeus might have considered these plants to be hybrids.

The botanical exploration of India by the British in the early 1800s led to the discovery of the first Asian species: *Circaea repens*, which Wallich (1832) named without describing, and *C. cordata*, which was described and illustrated by Royle in 1834. Despite the fact that European botanists had visited Japan prior to the time of Linnaeus (Ohwi, 1965), it was not until 1843 that the common and widespread *C. mollis* was described by Siebold and Zuccarini and not until 1859 that Maximowicz recognized *C. lutetiana* subsp. *quadrisulcata* as being distinct from the primarily European subsp. *lutetiana*.

Ascherson and Magnus prepared a detailed monograph of *Circaea* in 1870. Their paper showed remarkable insight in spite of the relatively few specimens available to them at the time; in fact, their observations on *C. cordata* were restricted to only the description and illustrations of Royle alone, and for *C. lutetiana* subsp. *canadensis* they saw only seven specimens! They did, however, have *C. mollis* in cultivation and were able to make first-hand observations of the living plants. Ascherson and Magnus were the first to recognize the importance of bracteoles in distinguishing the subspecies of *C. lutetiana*. They also recognized the distinctiveness of *C. alpina* subsp. *imaicola* and provided a description for Wallich's *C. repens*. In 1871 they distinguished and named *C. pacifica* (now *C. alpina* subsp. *pacifica*).

In 1879 Franchet and Savatier named *Circaea erubescens* and in 1910 the last species of *Circaea*, *C. glabrescens*, became known. It was described first as a variety of *C. cordata* by Pampanini.

The various papers by H. Léveillé between 1899 and 1912 added little to the understanding of the genus but did serve to point out the distinctiveness of *C. alpina* subsp. *angustifolia* (*C. lutetiana* race *erubescens* var. *mairei* of H. Léveillé, 1912).

In the twentieth century, with an increase in fieldwork in eastern Asia and the resulting increase in numbers of specimens available for study, most of the work in *Circaea* has led to the recognition of additional infraspecific taxa and an awareness of hybridization in the genus. Komarov (1905) recognized plants from

Manchuria as being distinct from *C. alpina* and called them var. *caulescens*. In 1933, Handel-Mazzetti provided a brief treatment of *Circaea* for China, including a key, brief descriptions of the taxa, and a list of the specimens that were known to him. He did, however, recognize very slender-leaved plants of *C. alpina* from Yunnan as distinct and called them *C. imaicola* var. *angustifolia* (here treated as *C. alpina* subsp. *angustifolia*). Handel-Mazzetti failed to notice that they intergrade completely with H. Léveillé's *C. lutetiana* race *erubescens* var. *mairei*. He also raised *C. cordata* var. *glabrescens* Pampanini to the rank of species, as it has been regarded subsequently. Handel-Mazzetti was the first to suggest hybridization between the Asian species of the genus when he named *C.* × *hybrida*, although it is now known that the plants on which he based this name are actually *C. cordata*.

Hara, in 1934, published the first of a series of papers dealing with *Circaea*, entitled *Observationes ad Plantas Asiae Orientalis* III, which provided keys and brief discussions for the taxa in Japan, Korea, Taiwan, and Manchuria. This work is important in that it is the first to illustrate clearly the differences in the fruits of several of the Asian species. In a subsequent paper, Hara (1936) described *C.* × *dubia*, although questioningly, as a possible hybrid between *C. cordata* and *C. erubescens*. Later, he (Hara, 1939, 1952) elaborated on the earlier work of Fernald (1915) concerning the similarity of *Circaea lutetiana* subspp. *canadensis* and *quadrisulcata* in eastern North America and in eastern Asia. These papers served to show that these two subspecies are much more closely related to each other, despite their wide disjunction, than either is to *C. lutetiana* subsp. *lutetiana* in Europe. In 1959 Hara reported on hybridization in the genus on a worldwide scale but with a greater emphasis on *Circaea* in eastern Asia (see above under hybridization).

Recently, Skvortsov (1970a, 1970b, 1977, 1979) has contributed accurate and useful observations on *Circaea* in Soviet Eastern Asia, in the Caucasus Mountains, and in the Himalayas, and has pointed out the distinguishing features of *C. alpina* subsp. *micrantha* from the latter region.

MORPHOLOGICAL CHARACTERS

The following characters are those which have been found to be the most useful in distinguishing the taxa of *Circaea* or, where not diagnostically useful, are in need of clarification. General shapes are based on terminology of simple symmetrical plane shapes (Systematics Association Committee for Descriptive Terminology, 1962). Measurements are from dried or spirit preserved material unless otherwise stated. Measurements enclosed by parentheses in the descriptions represent the extremes found in about 5% of the plants of a taxon.

Habit. All species of *Circaea* are erect, perennial herbs, although in some species there is a greater tendency for some plants to be decumbent at the base and to produce adventitious roots from the nodes and, less commonly, from the internodes. Decumbent plants are most often found in those species that grow in wet habitats such as *C. erubescens* and *C. mollis* or in those plants that are of hybrid origin. Hybrids involving *C. alpina* tend to be weak and fairly succulent and are especially prone to becoming decumbent.

Rhizomes. All species of *Circaea* produce subterranean rhizomes as the overwintering organ. The rhizomes are of two types and can be correlated with other morphological features. Species bearing bilocular fruits produce a number of rhizomes that are long and slender and sometimes branched towards their distal ends. At the end of the growing season the apical meristem of the rhizome becomes dormant and the entire system of rhizomes overwinters, giving rise to a single plant from each apex the following year. The rhizomes in these species never produce tubers at the tips.

In species bearing unilocular fruits the rhizomes are very slender to filiform and less commonly branched. Near the end of the growing season the terminal internodes cease to elongate and the terminal nodes are very closely spaced. This contracted, terminal portion of the rhizome eventually expands radially and forms a small tuber. In *Circaea alpina* the portion of the rhizome between the parent plant and the rhizome dies, leaving the tuber as the overwintering organ. Whether or not the proximal portion of the rhizome also dies in *C. repens* is not known. In addition to giving rise to the next year's plants, both types of rhizomes give rise to subsequent rhizomes from their distal nodes during the following year. *C. alpina* and hybrids involving *C. alpina* often produce stolons from the lowermost nodes of the stem. These aboveground stolons are morphologically indistinguishable from the subterranean rhizomes but frequently bear reduced leaves similar to the stem leaves. Eventually these stolons become subterranean at their tips.

Hybrids between bilocular and unilocular plants produce rhizomes that are morphologically intermediate between the two parents in having the terminal portion only slightly contracted, not nearly as thickened as in the tuber-producing parent and in having only a small proximal portion of the stolon dying at the end of the growing season.

A large majority of specimens lack carefully collected underground parts. The very few collections of *Circaea repens* with tubers still attached indicate that tubers in that species may be located a considerable distance below ground level.

Pubescence. Pubescence in *Circaea* consists of four basic hair types that vary independently on different parts of the plant. Type of pubescence is often useful alone or in combination with other characters in distinguishing groups of taxa (e.g., subspecies of *Circaea alpina*) and is especially useful in determining hybrid origins. The four basic types are as follows:

I. Long, straight, sharp-pointed, but soft, hairs. Hairs of this type are generally ca. 1 mm long but vary from 0.4 to 1.2 mm long. These are found in nearly all populations of *Circaea cordata*, in some populations of *C. lutetiana* subsp. *lutetiana*, and sporadically in *C. glabrescens*. Long, straight hairs are most abundant on the stems, petioles, leaves, buds, and abaxial surface of the sepals in *C. cordata*. Long hairs on the stem in *C. cordata* may continue into the inflorescence, where they are generally more sparse, or be replaced upwardly by other types of hairs. In hybrids involving *C. cordata* a few long hairs usually occur on some part of the plant but are often unevenly distributed and intermixed with other types of hairs. Long hairs, when present on the buds of hybrids, are a good indication that *C. cordata* is one of the parents.

Plants of *Circaea lutetiana* subsp. *lutetiana*, which were described by Beck (1893) as var. *villosa*, exhibit this type of pubescence on the stem. These plants

occur sporadically throughout the range of *C. lutetiana* subsp. *lutetiana*. Long hairs are absent in *C. lutetiana* subsp. *canadensis* and subsp. *quadrisulcata*.

In *C. glabrescens*, long hairs are occasionally found on the buds.

Besides variation in length, long hairs may be more or less curved above the middle. On dried specimens the hairs become flattened and twisted and appear to be multicellular.

II. Short, soft, falcate hairs ca. 0.2 mm long. This type of trichome is recurved when present on the stem and upwardly curved on the petioles and is found in at least some populations of all taxa. Falcate hairs on the stem are particularly useful in recognizing subspecies of *Circaea alpina* where they are correlated with less easily described characters.

Falcate hairs are usually very dense on the stem in *Circaea mollis* and *C. lutetiana* subsp. *lutetiana* and are found intermixed with long straight hairs on the stem of *C. cordata*. In some populations of *C. erubescens* from Japan and Cheju-do Island, Korea, the falcate hairs are ca. 0.1 mm long and give a dust-covered appearance to the stem under magnification. Plants of *C. erubescens* from the Asian mainland and most populations from elsewhere are glabrous, however. *Circaea alpina* subsp. *pacifica* may have the falcate hairs reduced to only a few, while the usually glabrous-stemmed *C. lutetiana* subsp. *quadrisulcata* may have sparse recurved hairs on the upper part of the stem just below the inflorescence. *C. glabrescens* has sparse to dense falcate hairs on the stem. *C. lutetiana* subsp. *canadensis* and *C. alpina* subsp. *alpina* and most populations of subsp. *micrantha* have the stem glabrous.

III. Capitate and clavate-tipped glandular hairs ca. 0.2 mm long. These hairs are more or less obvious in the inflorescence of nearly all taxa. The hairs are of a single basic type, varying from merely blunt and slightly thickened at the apex to conspicuously capitate. In life they exude a minute but conspicuous, viscid droplet and are especially noticeable in all subspecies of *Circaea lutetiana* and in some populations of *C. mollis*. Glandular hairs are absent in *C. erubescens*, in all populations of *C. alpina* subsp. *caulescens*, and in some populations of *C. alpina* subspp. *angustifolia* and *alpina*.

IV. Stiff uncinate hairs. These hairs are almost totally restricted to the fruit surface and vary in length proportionately to fruit size, ranging from ca. 0.5 to 1.2 mm long. Infrequently they may be found on the upper portion of the pedicel and rarely, in *Circaea cordata*, intermixed with other hairs in the inflorescence. According to Haberlandt (1912) they are unicellular and thick-walled. The uncinate hairs are clear and translucent in all taxa except *C. alpina* subsp. *angustifolia* and a few populations of *C. alpina* subsp. *micrantha*, which have uncinate hairs containing purple pigment. At anthesis the uncinate hairs are soft and short but continue to grow as the fruit develops. In all plants of *C. alpina* subsp. *micrantha* and in a few populations of *C. alpina* subsp. *alpina* and subsp. *imaicola* uncinate hairs are absent from the ovary at anthesis but begin development as the fruit begins to mature after the falling of the floral tube. The hooked hairs easily attach to the fur of animals, to clothing, and to other rough surfaces, no doubt aiding greatly in fruit dispersal.

Leaves. Leaf characters are only moderately useful as diagnostic characters in *Circaea*. In most species of the genus the leaves are ovate in shape with

rounded to cordate bases and acuminate apices. They are commonly deep green, thick, and opaque except in the most advanced subspecies of *C. alpina* (subspp. *alpina*, *micrantha*, and *pacifica*), where they are pale green and translucent. Leaf margins range from nearly entire to sharply serrate with the greatest variation occurring within *C. alpina*. *C. alpina* subsp. *angustifolia* has leaves that range from elliptic to trullate to narrowly ovate in shape and with bases that are narrowly to broadly cuneate. *Circaea mollis* also has leaves that are commonly cuneate at the base.

Inflorescence. The inflorescence in *Circaea* varies from a simple terminal raceme to a branched panicle of racemes. In addition, simple racemes or branched paniculate racemes are often produced from the tips of the uppermost axillary branches or directly from the uppermost axils. *Circaea cordata* and especially *C. mollis* bear numerous axillary inflorescences. In *C. glabrescens* and less often in *C. cordata* the branches of the terminal inflorescence are oppositely or suboppositely arranged while in other species they are usually alternate. *Circaea erubescens* has the lateral inflorescence branches lax and often unequal in length on a single individual and the inflorescence has a spindly appearance. In other species the inflorescence branches are commonly equal in length, straight and equally ascending.

Flowers. The flowers of *Circaea* fall into two major groups based on the presence or absence of an exserted nectary. In the primitive, outcrossing *C. cordata* and *C. glabrescens*, the inbreeding *C. alpina*, and in *C. repens* the nectary is within the floral tube, but completely fills its lower portion. In the remainder of the species the nectary is exserted beyond the opening of the floral tube forming a fleshy disc that completely encloses the style. Nectariferous tissue in these species also completely fills the floral tube. Hybrids between species with included and excluded nectaries always have the nectary present as a low ring at the summit of the floral tube. The nature of the nectary, especially in hybrids, is much more easily determined in living plants. In specimens without flowers but with nearly mature buds the nature of the nectary can be determined under magnification by passing a concentrated beam of light through the unopened bud. The nectary is usually very clearly seen by this method. This was also noticed by Gagnepain (1916).

The petals of *Circaea* are either white or pink and may be either constant or variable in color within a single species. *Circaea cordata* and *C. mollis* have consistently white petals while in *C. erubescens* they are nearly always pink. *Circaea glabrescens*, based on living plants in western Hubei, China, label data, and flower color in dried specimens appears to have consistently pink petals. Coloration of petals in some species, especially in *C. alpina*, may be habitat related with pink petals being produced in open, sunny habitats while white flowers are produced in shaded places. Petal shape is useful in a few species. The obtrullate to obovate, very shallowly notched petals of *C. erubescens* and the very deeply notched V-shaped petals of *C. repens* are distinctive, as are the emarginate to very shallowly notched petals of *C. alpina* subsp. *micrantha*.

Style measurements are from the summit of the ovary, including that portion of the style within the floral tube.

Fruit. Fruit characters are highly useful in distinguishing major groups and

individual species in *Circaea*. All species have fruits that are more or less densely covered with stiff, uncinate hairs and are well adapted to dispersal by attachment to passing animals. The corky tissue in the fruits of some species, especially in *C. lutetiana* subspp. *canadensis* and *quadrisulcata* and in *C. mollis*, may also be an additional aid to dispersal by water. The report by Christ (1912) that the fruits of *C. alpina* are violently thrown for some distance is erroneous. Fruits of *C. alpina* mature rapidly, however, and are more readily detached by light pressure than those of other species.

Circaea alpina and *C. repens* bear unilocular fruits while the remaining species have bilocular fruits. In both cases there is only a single seed in each locule. Freehand sections of the fruits of *C. repens* that I have examined contain a trace of a second locule, represented by a darkened line. There is no trace of an ovule in this remnant locule.

The fruits of *Circaea alpina*, *C. repens*, and *C. lutetiana* subsp. *lutetiana* are clavate in shape, lack corky tissue or have the corky tissue greatly reduced, and have a non-corrugated surface. Fruits of *C. cordata* are flattened orbicular or flattened pyriform in shape and contain longitudinal rows of corky tissue along the margins and between the locules, which show on the surface as low, rounded ridges. Fruits of *C. erubescens* and *C. glabrescens* are more or less ovate to pyriform in shape and, although both contain rows of corky tissue, the surface is smooth except for a shallow groove on the dorsal and ventral surfaces, which represents an extension of the pedicel. *C. lutetiana* subspp. *canadensis* and *quadrisulcata* and *C. mollis* have fruits that are pyriform to globose with prominent, corky thickened ribs and deep sulci. The rare fruits that develop in hybrids are usually intermediate between the two parents but occasionally resemble fruits of one parent more than the other. Fruit measurements are from dried specimens. In most cases this represents shrinkage of 10–15% from live plants. Length and width measurements for the fruits do not include the uncinate hairs.

Coloration of the stem. While difficult to use as a diagnostic character to separate species, coloration of the nodes is often useful in determining hybrid origins. *Circaea erubescens* consistently has the nodes reddened and, in life, the stems, and especially the nodes, are succulent and shining. *Circaea mollis* also has the nodes darkened but the usually dense pubescence of minute falcate hairs causes the nodes to appear dull. *Circaea cordata*, on the other hand, has green nodes. In hybrids between either *C. erubescens* or *C. mollis* and *C. cordata* the nodes are darkened but intermediate in intensity between the parents. *Circaea alpina* subsp. *alpina* may have either green or red nodes but hybrids with *C. erubescens* have nodes that are darker than in any *C. alpina* subsp. *alpina*. The coloration of the nodes in other species is less consistent and is an unreliable character.

Bracteoles. The presence or absence of a minute bracteole at the base of the pedicel is useful in separating taxa in a few cases but is generally unreliable. *Circaea lutetiana* subsp. *canadensis* may be distinguished from *C. lutetiana* subsp. *quadrisulcata* by the presence of such bracteoles. *Circaea alpina* subsp. *caulescens* is separated from other subspecies of *C. alpina* partly by its nearly constant lack of a bracteole. Several workers, from Ascherson and Magnus (1871) to Munz (1974) have stated that *C. alpina* subsp. *pacifica* lacks bracteoles and have used

this character to separate subsp. *pacifica* from other taxa of the genus, but I have found this to be very unreliable. The majority of specimens of *C. alpina* subsp. *pacifica* have bracteoles subtending at least a few pedicels.

In most species, bracteoles are present at the base of at least the three or four lowest pedicels of a raceme and represent progressively reduced leaves. When determining presence or absence of bracteoles it is best to examine only the middle or upper pedicels.

Systematic Treatment

Circaea L.

Circaea L., Sp. Pl. 8. 1753.

Ocimastrum Ruprecht, Fl. Ingr. 366. 1860. Nom. illegit., based on *Circaea* L.
Regmus Dulac, Fl. Hautes-Pyr. 328. 1867. Nom. illegit., based on *Circaea* L.
Carlostephania Bubani, Fl. Pyren. 2: 658. 1910. Nom. illegit., based on *Circaea* L.

Coarse or delicate, usually erect, perennial herbs, producing subterranean rhizomes at the base, these terminated by tubers late in the season in *Circaea alpina* and *C. repens*, which give rise to the following year's plants from the apex; stolons often also present from the lower nodes in *C. alpina*. Plants, except for fruits, totally glabrous (in some plants of *C. alpina* and *C. erubescens*) to densely pubescent with four basic types of trichomes: 1. short, soft, falcate hairs, 0.2–0.3 mm long, which are always recurved on the stems and upwardly curved on the petioles; 2. long, straight or slightly curved sharp-pointed, soft hairs 0.2–1.2 mm long (in *C. cordata* and some plants of *C. lutetiana* subsp. *lutetiana* and *C. glabrescens* and in some hybrids involving *C. cordata*); 3. short, soft, capitate and clavate-tipped, glandular hairs, 0.1–0.3 mm long; 4. stiff, translucent (containing purple pigment in most plants of *C. alpina* subsp. *angustifolia* and some plants of *C. alpina* subsp. *micrantha*), uncinate hairs, restricted to the fruits or sometimes on the upper portion of the pedicels. Leaves cauline, petiolate, opposite and decussate, horizontally spreading, flat or slightly drooping at the apex; one pair of leaves larger than the others and located from slightly below the middle of the stem to near the base of the inflorescence, the lowest leaves most commonly deciduous by flowering time. Stipules present, caducous or rarely persistent, setaceous or gland-like, green or darkened. Inflorescence terminal on the main stem and often also at the tips of the uppermost, reduced axillary branches or occasionally with the lateral inflorescences arising directly from the uppermost leaf axils. Inflorescence of simple or branched racemes, when branched the lateral racemes arising from near the base of the terminal raceme and subtended by reduced leaves or leaflike bracts. Pedicels erect in bud and clustered at the apex of the raceme, the raceme elongating and the pedicels becoming ± distantly spaced, divergent and perpendicular to the raceme axis prior to anthesis or, in most subspecies of *C. alpina*, erect or ascending at anthesis and the raceme elongating after the flowers open; horizontally spreading to strongly reflexed in fruit. Buds valvate, white, green, pink, or purple. Ovary unilocular or bilocular, with one seed per locule. Flowers 2-merous, bilaterally symmetrical, opening in the early morning, the stigma receptive before or shortly after anthesis; one anther

shedding pollen at anthesis, the other with ± delayed dehiscence. Floral tube, from a mere constriction at the summit of the ovary, to 2.4 mm long, subcylindric to funnelform, deciduous after maturity of the flower. Sepals two, white, green, pink, or purple abaxially, most commonly white or pink adaxially, spreading or reflexed in flower. Petals two, alternate with the sepals, white or pink, notched at the apex or, in *C. alpina* subsp. *micrantha*, subentire. Stamens two, opposite the sepals, shorter than, to equalling, the style; filaments white or pink, the same color as the petals, very narrowly clavate, attached to the floral tube near its mouth; anthers white, pink or very pale yellow, dorsifixed, longitudinally and introrsely dehiscent. Pollen yellow, shed as monads, 3-pored, rarely with a few 2- or 4-pored grains (in some plants of hybrid origin the pollen may commonly be 2-, 3-, 4-, and 5-pored with 3-pored pollen being somewhat more common), with smooth viscin threads, these often lacking in *C. alpina*. Style white or pink, usually the same color as the petals, filiform, embedded in nectariferous tissue at the base; stigma bilobed, white or pink, usually the same color as the petals, minutely papillate at maturity. Nectary wholly within and filling the lower portion of the floral tube or elongated and projecting above the opening of the floral tube as a fleshy, cylindrical or ring-like disc. Fruit an indehiscent capsule, deciduous with the pedicel at maturity, covered with soft to firm, translucent (containing purple pigment in most plants of *C. alpina* subsp. *angustifolia* and some plants of *C. alpina* subsp. *micrantha*), uncinate hairs; with or without internal, longitudinal rows of corky tissue, when present, these sometimes very conspicuous at maturity of the fruit. Seeds smooth, fusiform or, more commonly, broadly clavoid to slenderly ovoid, adhering ± firmly to the inner ovary wall. Gametic chromosome number, $n = 11$.

LECTOTYPE: *Circaea lutetiana* L.; Britton and Brown, Ill. Fl. N. U.S. ed. 2. 2: 610. 1913.

Distribution: Throughout the northern hemisphere in moist, temperate, broad leaved evergreen, deciduous, coniferous, and cool boreal forests. From sea level to 5,000 m elevation, and from 10° to 70° N. Lat.

Ascherson and Magnus (1870) divided *Circaea* into two groups, which they called "divisions," based on the number of locules in the fruit. Included in their *Uniloculares* are *C. alpina* and *C. repens*, with all other species placed in their *Biloculares*. These were later given sectional status by Steinberg (1949) but with the name *Biloculares* of Ascherson and Magnus changed to *lutetiana*. The single line of specialization leading from the bilocular, outcrossing species to the unilocular, self-pollinating *C. alpina*, linked by the intermediate *C. repens*, represents a continuum that makes the formal recognition of these two infrageneric groups unwarranted, especially in a genus of only seven species.

In this treatment, the species and subspecies of *Circaea* are treated in order of their specialization.

Hybrids, because of their widespread and frequent occurrence, are treated here in the same manner as the species and are provided with full descriptions and discussions. The intermediate nature of the hybrids between the parental species and the resulting confusion which they cause make it difficult to write a satisfactory key that will allow easy identification of all taxa. The absence of

quantitative differences between species adds to the difficulty. For those reasons, two separate keys are provided, one for all species excluding hybrids and the other including hybrids. In addition, separate keys are provided for the taxa in Europe and in North America.

Flowers, mature fruits, and carefully collected rhizomes are highly desirable to facilitate identification. The nature of the nectary is most easily determined in living plants.

Key to the Species, Excluding Hybrids

1a. Ovaries and fruits bilocular; rhizomes not terminated by tubers 2
  2a. Nectary wholly included within the floral tube, not projecting as a cylindrical or ringlike disc above the opening of the floral tube 3
    3a. Axis of inflorescence pubescent, with falcate, glandular, and long, straight or slightly curved, patent hairs; fruit obliquely thick lenticular to flattened pyriform, obliquely rounded to the pedicel ..... 1. *C. cordata*
    3b. Axis of inflorescence glabrous or with only glandular hairs; fruit obovoid to pyriform, not at all or only slightly flattened, tapering smoothly to the pedicel ..... 2. *C. glabrescens*
  2b. Nectary exserted beyond the floral tube, projecting as a cylindrical or ringlike disc above the opening of the floral tube 4
    4a. Petals obovate to depressed broadly obovate, notched one quarter or more their length; axis of inflorescence and pedicels commonly pubescent 5
      5a. Fruits with prominently thickened ribs and sulci, broadly obovoid, pyriform, or subglobose, tapering obliquely or rounded to the pedicel; floral tube 0.4–1.2 mm long; plants of North America, eastern Asia and westward between 50° and 60° N. Lat. in the U.S.S.R. to the vicinity of Moscow 6
        6a. Stem pubescent, often densely so, with falcately recurved hairs; leaves cuneate, rarely rounded at the base; petals 0.7–1.8 mm long; inflorescence subglabrous or pubescent, with glandular and falcately recurved hairs ..... 3. *C. mollis*
        6b. Stem glabrous or with very sparse, falcately recurved hairs; leaves rounded to subcordate at the base; petals (1.3–)1.9–2.9 mm long; inflorescence densely glandular pubescent, without falcately recurved hairs ..... 4. *C. lutetiana*
      5b. Fruits without prominently thickened ribs and sulci, broadly clavate to slender obovoid, tapering smoothly to the pedicel; floral tube (0.8–)1.1–2.4 mm long; plants of central and western Europe and south of 50° N. Lat. in southwestern Asia ..... 4. *C. lutetiana*
    4b. Petals obtrullate, notched one fifth or less their length; axis of inflorescence and pedicels glabrous ..... 5. *C. erubescens*
1b. Ovaries and fruits unilocular; rhizomes terminated by tubers 7
  7a. Petals notched more than one half their length, V-shaped; pedicels glandular pubescent; combined length of mature fruit and pedicel, (6.8–)7.5–15 mm long; leaves with 9–15 secondary veins ..... 6. *C. repens*
  7b. Petals notched one half or less their length, obovate to obtriangular; pedicels glabrous; combined length of mature fruit and pedicel, 3.5–7.8 mm long; leaves with 4–10 secondary veins ..... 7. *C. alpina*

Key to Species and Hybrids

1a. Ovary bilocular; rhizomes without tuberous thickenings 2
  2a. Nectary wholly within the floral tube, not present as a cylindrical or ringlike disc projecting above the opening of the floral tube 3
    3a. Axis of inflorescence pubescent, often densely so, with falcate, glandular and long, straight or slightly curved, patent hairs; fruit obliquely lenticular to flattened pyriform, obliquely rounded to the pedicel ..... *C. cordata*
    3b. Axis of inflorescence glabrous or with only sparse, glandular hairs, fruit obovoid to pyriform, not at all or only slightly flattened, tapering smoothly to the pedicel ..... *C. glabrescens*

2b. Nectary exserted beyond the opening of the floral tube, projecting as a cylindrical or ringlike disc above the opening of the floral tube 4
4a. Petals obovate to depressed broadly obovate, notched one quarter or more their length; axis of inflorescence with at least a few glandular or falcate hairs 5
5a. Stem with darkened nodes, the nodes purple or brown 6
6a. Stem glabrous below the inflorescence 7
7a. Leaves prominently toothed, sharply dentate to serrate 8
8a. Inflorescence and often pedicels glandular pubescent ..... *C.* × *intermedia*
8b. Inflorescence and pedicels glabrous ..... *C.* × *mentiens*
7b. Leaves denticulate, the teeth low and inconspicuous 9
9a. Commonly all fruits developing to maturity; fruits with prominent ribs and deep sulci ..... *C. lutetiana*
9b. Commonly no fruits developing to maturity; fruit, when present, with only low ribs and very shallow sulci ..... *C.* × *decipiens*
6b. Stem pubescent below the inflorescence 10
10a. Sepals purple; petals often pink 11
11a. Plants with at least a few, long, straight, or slightly curved, patent hairs on some part of the plant in addition to falcate and glandular hairs; leaves rounded to subcordate at the base 12
12a. Plants fertile; Europe and southwestern Asia ..... *C. lutetiana*
12b. Plants highly sterile; eastern Asia ..... *C.* × *skvortsovii* and *C.* × *dubia*
11b. Plants without long, straight or slightly curved patent hairs, with only short, falcate and glandular hairs; leaves broadly cuneate to subcordate at the base 13
13a. Plants fertile ..... *C. lutetiana*
13b. Plants highly sterile 14
14a. Leaves rounded to subcordate at the base; pollen less than 1% fertile ..... *C.* × *intermedia*
14b. Leaves broadly cuneate to rounded at the base; pollen usually 1–20% fertile ..... *C. erubescens* × *C. mollis*
10b. Sepals green; petals white 15
15a. Leaves cuneate at the base; plants without long, straight or slightly curved, patent hairs, with only falcate and glandular hairs ..... *C. mollis*
15b. Leaves rounded at the base; plants with at least a few, long, straight or slightly curved, patent hairs in addition to falcate and glandular hairs ..... *C.* × *ovata*
5b. Stem without darkened nodes, green throughout except sometimes buds, sepals and petals 16
16a. Stem glabrous below the inflorescence 17
17a. Leaves prominently toothed, dentate to serrate ..... *C.* × *intermedia*
17b. Leaves shallowly toothed, denticulate ..... *C. lutetiana*
16b. Stems pubescent below the inflorescence ..... *C. lutetiana*
4b. Petals obtrullate, notched one fifth or less their length; axis of inflorescence glabrous ..... *C. erubescens*
1b. Ovary unilocular; rhizomes sometimes with terminal tuberous thickenings 18
18a. Nectary included within the floral tube 19
19a. Pedicels pubescent with glandular hairs 20
20a. Pedicels spreading at anthesis, the flowers loosely spaced ..... *C. repens*
20b. Pedicels ascending at anthesis, the flowers somewhat clustered ..... *C. alpina* subsp. *imaicola* × *C. repens*
19b. Pedicels glabrous ..... *C. alpina*
18b. Nectary exserted beyond the opening of the floral tube as a low, fleshy, ringlike disc 21
21a. Nodes deep purple; eastern Asia ..... *C.* × *mentiens*
21b. Nodes pale purple or green; widespread in Europe and North America, rare in eastern Asia ..... *C.* × *intermedia*

KEY TO CIRCAEA IN NORTH AMERICA

1a. Flowers opening after elongation of the raceme axis, more or less loosely spaced, borne on spreading pedicels; fruits obovoid to pyriform or the fruits sterile and aborting shortly after anthesis 2

2a. All, or nearly all, ovaries developing to maturity; fruit with corky thickened ribs separated by deep grooves; pollen highly fertile ..... *C. lutetiana* subsp. *canadensis*
2b. All ovaries aborting shortly after anthesis, very rarely a few persistent after anthesis; fruit, when somewhat persistent, with only low ribs and with shallow grooves; pollen highly sterile ..... *C. × intermedia*
1b. Flowers opening before elongation of the raceme axis, clustered and corymbiform at the apex of the raceme, borne on erect or ascending pedicels; fruits clavate 3
3a. Plants with at least a few, recurved, falcate hairs on the stem; leaves subentire or very minutely denticulate, rounded to truncate, rarely subcordate at the base ..... *C. alpina* subsp. *pacifica*
3b. Plants with the stem completely glabrous; leaves prominently denticulate to serrate, cordate, rarely rounded at the base ..... *C. alpina* subsp. *alpina*

KEY TO *CIRCAEA* IN EUROPE

1a. Axis of inflorescence elongating before the flowers open; the flowers on spreading or slightly ascending pedicels; rhizomes without terminal tuberous thickenings; nectary exserted beyond the opening of the floral tube 2
2a. Plants fertile with full fruit set and with more than 70% filled pollen grains 3
3a. Fruit with deep sulci and prominent ribs, obovoid, pyriform or globose; stem glabrous; primarily from Moscow in the U.S.S.R. eastward ..... *C. lutetiana* subsp. *quadrisulcata*
3b. Fruit without deep sulci and prominent ribs, clavate to obovoid, stem commonly pubescent; primarily from Moscow westward throughout Europe and in southwestern Asia, North Africa ..... *C. lutetiana* subsp. *lutetiana*
2b. Plants sterile, rarely setting fruit and with fewer than 2% filled pollen grains ..... *C. × intermedia*
1b. Axis of inflorescence elongating after the flowers open; the flowers on erect or ascending pedicels; rhizomes with terminal tuberous thickenings; nectary wholly within the floral tube ..... *C. alpina* subsp. *alpina*

1. Circaea cordata Royle, Illustr. Bot. Himal. 211, *t. 43, fig. 1, a–i.* 1834.—FIG. 3.

Circaea mollis sensu Maximowicz, non Siebold & Zucc., Prim. Fl. Amur. 105. 1859.
Circaea cardiophylla Makino, Bot. Mag. Tokyo 20: 42. 1906. TYPE: Japan, Honshu, Prefecture Tokyo, Dokan-yama, *T. Makino MAK 6904* (MAK, lectotype).
Circaea bodinieri H. Lév., Bull. Acad. Int. Géogr. Bot. 22: 224. 1912. nom. provis.
Circaea × hybrida Hand.-Mazz., Symb. Sin. 7: 605. 1933. TYPE: China, Yunnan, Mekong-Salwin divide, 28°10′ N. Lat., September 1914, *G. Forrest 13254* (E, holotype).
Circaea kitagawae Hara, J. Jap. Bot. 10: 595. 1935. TYPE: China, Hopeh, Ch'engte ("Manchuria, Jehol"), between Hsing-lung-t'ang and Pei-ying-fang, 27 August 1933, *T. Nakai, M. Honda & M. Kitagawa* (TI, holotype).

Plants usually robust, 2–15 dm tall, simple or, more commonly branched above, forming numerous, often branched, non-tuberous rhizomes, which give rise to the following year's plants from their tips. Plants pubescent, usually densely so. The stems with long, patent or slightly bent, sharp-pointed, soft hairs, 0.5–1.4 mm long, soft, short, falcately recurved hairs, 0.2–0.3 mm long, and short, capitate and clavate-tipped glandular hairs, 0.2–0.4 mm long, the ratios of these hair types varying greatly between populations. The axis of the inflorescence with hairs as on the stem but more often with a greater proportion of short, falcately recurved and glandular hairs. The petioles with hairs as on the stem but with the falcate hairs upwardly curved. The leaves with long straight hairs, 0.4–1.1 mm long, along the veins, and commonly also on the interveinal areas, on both surfaces, the shorter, straight hairs often appearing strigillose in pressed specimens, also with falcate hairs and long, straight hairs along the margin. Stems green. Leaves horizontally spreading, drooping at the tips, green, opaque. Median leaves the largest, 4–11(–13) cm long, (2.3–)3.5–7(–11) cm wide. Leaves becoming gradually reduced in size upward to the base of the inflorescence and ultimately bract-

FIGURE 3. *Circaea cordata* Royle.—A. Mid-stem node.—B. Habit.—C. Flower with petal removed; note absence of exserted nectary.—D. Inflorescence.—E. Fruit. From *Boufford et al. 19575* (CM, KYO, MHA, MICH, MO, NCU, S).

like and alternate, gradually reduced in size downward (although not often apparent since the lower leaves are usually deciduous by flowering time). Leaves narrowly to very broadly ovate, short acuminate, very broadly cuneate, broadly rounded to truncate or, more commonly, cordate at the base, denticulate to subentire. Petioles terete, (1–)2–7(–10) cm long, with, or occasionally without, reduced branches arising in the axils. Inflorescence densely pubescent with short, soft, falcately recurved hairs and with short, capitate and clavate-tipped, glandular hairs, often with irregularly occurring, long, straight or slightly bent hairs intermixed; terminal on the main stem and at the tips of the short, uppermost axillary branches or occasionally the lateral racemes arising directly from the uppermost leaf axils. The racemes simple or the terminal, less often the laterals, freely branched near the base. The terminal raceme, from the uppermost reduced leaf or leaf-like bract, ca. 2 cm long at initiation of flowering, to 20 cm long at cessation of flowering; lateral racemes ca. 2 cm long at initiation of flowering, to 15 cm long at cessation of flowering, subequal in length on the same plant. Flowering pedicels 0.7–2 mm long, perpendicular to the axis of the raceme at anthesis and ± clustered, pubescent, with capitate and clavate-tipped glandular hairs 0.1–0.2 mm long, intermixed with long, straight, sharp-pointed soft hairs, 0.4–0.9 mm long, occasionally also with uncinate hairs as on the ovary; with a minute setaceous bracteole, 0.4–1 mm long at the base. Fruiting pedicels 1.5–2.8 mm long. Buds pubescent, rarely subglabrous, with few to many long, straight or slightly curved, rarely hooked, hairs, 0.4–1.1 mm long, and with straight, capitate and clavate-tipped glandular hairs, 0.1–0.2 mm long; green or white; narrowly to broadly elliptic to obovoid, smoothly rounded to the obtuse apex; from the summit of the ovary, 2.5–4.3 mm long, 1.3–2 mm thick just prior to anthesis. Ovary 1–1.5 mm long, 0.6–0.9 mm thick at anthesis, broadly elliptic to subcircular in outline, often obliquely rounded to the pedicel, dorsally flattened, very densely pubescent with translucent or white, soft, uncinate hairs. Floral tube 0.6–1 mm long, 0.2–0.4 mm thick at the narrowest point, funnelform to broadly so, sometimes tapering concavely to the base, pubescent, with short, capitate and clavate-tipped, glandular hairs, 0.1–0.2 mm long, and sometimes also with long, straight hairs as on the buds. Sepals 2–3.7 mm long, 1.4–2 mm wide, pubescent abaxially with hairs as on the buds, white or pale green; ovate to broadly so, broadly to narrowly rounded to the obtuse apex; reflexed in flower. Petals 1–2.4 mm long, 1.2–3.1 mm wide, wider than long, white, depressed obovate to very broadly obovate in outline, the apex obcordate; the apical notch 0.5–1.9 mm deep, ½–⅔ the length of the petal, the petal lobes broadly rounded; the petals broadly rounded to the usually short clawed base. Stamens spreading at anthesis, shorter than, to equalling the style; filaments 1.5–3.5 mm long; anthers 0.5–0.7(–1) mm long, 0.3–0.6 mm thick. Style straight, erect or slightly depressed at the tip, 3–5(–5.5) mm long, topped by an obtriangular to transversely oblong, bilobed stigma, 0.2–0.3 mm tall, 0.5–1 mm thick. Nectary wholly within the floral tube and inconspicuous. Mature fruit 3–3.9 mm long, (1.8–)2.2–3.3 mm thick, bilocular and 2-seeded, obliquely obovoid to lenticular, dorsally flattened, broadly rounded at the apex, truncate or, most often, obliquely rounded to the pedicel; with low, corky thickenings along the margins and between the locules, without prominent sulci; densely covered with stiff, translucent, uncinate hairs, 0.8–1.2 mm long,

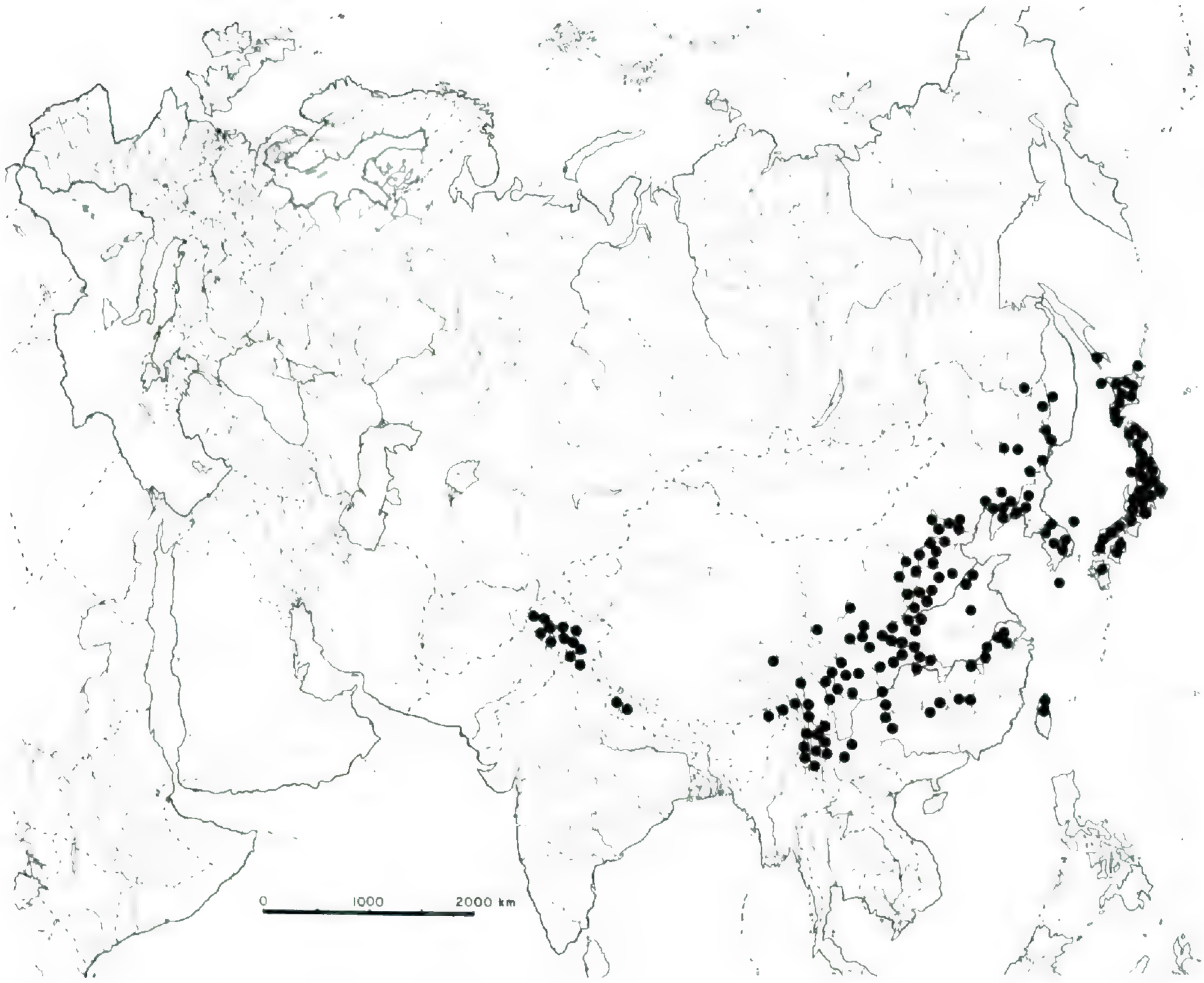


FIGURE 4. Distribution of *Circaea cordata* Royle.

and with fewer, often hidden, capitate and clavate-tipped glandular hairs, 0.1–0.2 mm long. Fruiting pedicels reflexed, often sharply so. Combined length of pedicel and mature fruit, 4.4–7 mm long. Gametic chromosome number, $n = 11$.

TYPE: India, Kotgarh, *J. Royle* (LIV, lectotype; photograph at MO. K, probable isolectotype).

Distribution (Fig. 4): Dry mesic slopes and well drained soils in mixed deciduous forests, barely extending into the southern part of the transition zone between deciduous and boreal forests. Japan; southeastern Siberia, Korea, and northeastern China, southwestward to Sichuan and Yunnan, China, and Assam, India; Nepal; northwestern India to Kashmir and Pakistan; Taiwan. From sea level to 3,500 m. Flowers mid-June to mid-August.

Representative specimens examined:

U.S.S.R.

RUSSIAN S.F.S.R. Vladivostok near Sedanka Station, *S. J. Enander in 1926* (S); Flora Amurensis, *V. Komarov in 1895* (LD); Khabarovsk District, along Amur valley, *I. W. Kuznezow 631* (DS); Vladivostok District, S shore of Lake Chauka, E of Nova-djevilsa, *G. Melvil in 1926* (DS, S); Sakhalin, Holmsk District, *M. Pimenov 1095* (DS); Khabarovsk Province, Bikin District, near Bikin, *L. S. Plotnikova in 1967* (MHA); Kurile Islands, Kunashiri Island, Tretyakova, *A. Schroeter 915a* (MHA); Primorski Province, near Vladivostok, *V. N. Voroshilov in 1958* (DS).

ASIA

CHINA. ANHUI: Huang Shan, *S. S. Chien 1281* (W), *R. C. Ching 8598* (E, UC, US), *K. S. Chow 131* (A, K, KYO, MO, NCU, PE); Chiu Hwa Shan, *C. S. Fan & Y. Y. Li 174* (E, K, NAS); Huang Shan, *T. N. Liou & Tsoong 2543* (E, PE); Chiuhwa Shan, *S. C. Sun 1228* (NY); Jung Hsien, *without collector 458* (NAS). GANSU: Tianshui Hsien, *C. W. Chang 235* (NAS, PE); Tianchi Shan, *W. Y. Hsia 5966* (PE); border of E Gansu & N Sichuan, *G. Potanin in 1885* (LE); Huating Hsien, *T. P. Wang 17007* (PE). GUIZHOU: San-chouer, *J. Cavalerie 3781* (E, P); Zunyi Hsien, *Guizhou Exped. 1288* (PE); Dutun Hsien, near Hai-kow, *Y. Tsiang 5804* (NAS, NY, PE, S, UC, W); Tsun-i, Chin-ting Shan, *C. C. Tui 1288* (PE). HEBEI: Beijing, *A. David s.n.* (BM); San Shan, *N. Desoulavy 580* (LE); Neiqui, *S. Y. Lau 694* (NAS); Zan-huang, *S. Y. Lau 823* (NAS); Pingshan Hsien, *A. R. Li 1149* (PE); Miofeng Shan, *C. F. Li 72* (PE); Tang Hsien, *K. M. Liou 3082* (NAS); Fuping Hsien, *K. M. Liou 3551* (PE); Neiqui Hsien, *X. Y. Liu 694* (PE); East Tomb, *Y. Liu 11880* (PE); Neiqui, *Y. Liu 13030, 13236* (NAS); Moryo-san, *T. Nakai et al. in 1933* (TI); Changshanyü, *T. Nakai et al. in 1933* (TI); Chengde Shi, *Nankai Univ. 256* (PE); Xiaowutaishan ("Hsiao-wu-t'ai-shan), Tung-lin, *H. Smith 231* (LD, S, UPS); East Tomb, *T. Tang 2202* (PE); Xiaowutaishan, *C. W. Wang 60792* (PE); Yang-chia-ping, Xiaowutaishan, *C. W. Wang 61827* (PE); Trappist Monastery, *C. G. Yang 171* (PE); Daxing Hsien, *C. G. Yang 1014* (PE); Yong-ning, *without collector A418* (S). HEILONGJIANG: opposite Harbin, Siaolin, *Jettmar in 1926* (W); Ch'i-li, P'ai-ta, near Hsuenhwa, *H. Serre 9523* (W); Rache Hsien, *K. C. Wang 603, 668* (PE); "Heilongjiang," *Y. Yabe in 1917* (NAS). HENAN: Xixia, *Exped. Henan 1189, 1273* (NAS); Song Hsien, *Exped. Henan 2236* (NAS); Mt. Ch'i-feng Shan, *Fr. Hugh in 1899* (BM); Lushi Hsien, *K. M. Liou 4656, 4705* (PE). HUBEI: Shennongjia, *K. S. Chow 76112* (PE); Yichang, *W. Y. Chun & S. S. Chien 5150* (UC); Badong Hsien, *H. C. Chow 916* (E, NY, PE); Hsing-shan, *A. Henry 6552* (K); "Hupeh," *A. Henry 6573* (BM, G, K); Xingshan Hsien, *H. J. Li 2960, 1139* (PE); Zhuxi, *P. Y. Li 2970* (NAS); Shennongjia, *Shennongjia Exped. 32724* (PE); Chiang-yang, *E. H. Wilson 1545* (E, K, LE, NY, US); Hsing Shan, *E. H. Wilson 1545* (W). HUNAN: Mt. Yün-shan near Wu-kang, *H. Handel-Mazzetti 12317* (E, LE, W); Nanyue, *K. C. Kuan & B. M. Yang 118* (PE); Nanyue, Shang-feng-shih, *Y. Liu 169* (PE). JIANGXI: Shangyou Hsien, *T. L. Chin 70537* (PE); Lushan, *K. C. Kuan 74356* (PE), *A. N. Steward 2633* (K, MO, NY, UC, US); Kuling, Mt. Lu Shan, *A. N. Steward 4696* (MT). JILIN: Antu Hsien, *P. Y. Fu 2595* (PE); Lungtan Shan, *Y. C. Ma 10144* (PE). LIAONING: Anshan city, Chien-shan-chung kou, *I. L. Chou et al. 2595* (PE); Anshan, *P. Y. Fu 2595* (PE); Shen-yang (Mukden), *Litvinov 3173* (GH); Fentei, *Y. Yabe in 1909* (NAS); Quiansha, *Y. Yabe in 1909* (NAS); Caohekou, *Y. Yabe in 1917* (NAS). SHAANXI: Tai hua Shan, *K. S. Hao 3829* (PE); Huashan, *K. S. Hao 3927* (PE); Cho-toe-miao, Hu Hsien, *Fr. Hugh s.n.* (BM); Nungshan Hsien, *H. W. Kung 3130* (PE); Hu Hsien, *P. C. Kuo 96, 448* (PE); Taibai Shan, *T. N. Liou 48* (NAS, PE), *1741* (PE); Baoji Hsien, *C. H. Wang 110* (PE); Lanian Hsien, *T. P. Wang 16001* (PE); Chungnan Shan, *T. P. Wang 2103* (PE); Taibai Shan, *T. P. Wang 1473, 1739* (PE). SHANDONG: Linqu Hsien, *T. Y. Chou 5304* (NAS); Zibo Hsien, *T. Y. Chou 5658* (NAS); Tai Shan, *T. Y. Chou 7202* (NAS), *Exped. Wil. Pl. Shandong 7122* (NAS). SHANXI: Jincheng Hsien, *S. Y. Bao 414, 1625* (PE); Huangqu Hsien, *S. Y. Bao 2067, 2137* (PE); Ruicheng Hsien, *S. Y. Bao 857* (PE); Fou-p'ing, *L. Chavet 690* (W); Xing Hsien, *Huanghe Exped. 2582* (PE); Wutai Shan, *K. C. Kuan & Y. L. Chen 2520* (PE); Qin Hsien, *K. C. Kuan & Y. L. Chen 887, 956, 1078* (PE); Lien-nan Hsien, *E. Licent 2263* (K, W); Wei-tze-p'ing, *E. Licent 2523* (K, P); Yao-shan, Hsia-ch'uan, *E. Licent 12550* (W); Lingchuan Hsien, *K. M. Liou 7621* (PE); Pingting Hsien, *K. M. Liou 3980* (PE); route of Wu-tai, Yang-t'ao-li, *A. Serre A690* (UPS); Yuan-chu, Yang-shu-ling, *H. Smith 6163* (S, UPS); Yuan-chu, Shui-wang-p'ing, *H. Smith 6736* (UPS); Chieh-hsiu, Ch'o-mei-shan, *H. Smith 7619* (LD, S, UPS); Xi Hsien, Shilo Shan, *T. P. Wang 3055* (K, PE); Huo Hsien, *T. P. Wang 3967* (PE). SICHUAN: Fenjie Hsien, *C. C. Chang 25720* (PE); Nanchuan, *T. Y. Chang 5720* (NAS); Fenjie, *H. F. Chow 26941* (NAS); Mao Hsien, *H. F. Chow 26941* (PE); Baoxing Hsien, *K. L. Chu 3664* (BM, E, PE); Dunggo, *K. L. Chu 7855* (PE); Chengkou Hsien, *T. L. Dai 101867, 104176, 105726, 105913* (PE); "Tchen-keou," *R. P. Farges s.n.* (P, US); Li Hsien, *C. Ho 5770* (NAS); Shimian Hsien, *C. C. Hsieh 42285* (PE); Kangding, *C. P. Huang 988* (PE); Mt. Emei Shan ("Uo-mi-san"), *Fr. Hugh in 1899* (BM); Heichui, *H. Li 23747, 23780* (NAS); Dajin, *H. Li 78052, 78224, 78638* (NAS); Nanchuan, *K. F. Li 63456* (NAS), *63482* (NAS, PE); Chengkou, *P. Y. Li 3725* (NAS); Heishui Hsien, *X. Li 73747, 73780* (PE); Dajin Hsien, *X. Li 77977* (PE); Nanchuan, *C. Pei 8198* (NAS); between Baor & Tha, *H. Smith 4893* (S, UPS); Chengkou, *T. L. Tai 103177, 104176, 105913* (NAS); SE of Mao Hsien, *F. T. Wang 21907* (G, PE); N of Chengdu Plain, *F. T. Wang 22108* (G); Nanchuan, *F. T. Wang 22108* (NAS); Chengdu, *F. T. Wang 22108* (PE); Leipo Hsien, *T. T. Yü 3401, 3685* (PE). TAIWAN: Taichung Hsien, Chika, *T. C. Huang & C. F. Hsieh 7281* (TAI); Taichung Hsien, Li Shan, *G. Ikeda 1712* (KAG); Hsinchu Hsien, Ta-pa-chien-shan, *C. S. Kuoh 3227* (TAI); Taichung Hsien, Wuse ("Use"), *E. Matsuda s.n.* (TAIF); Hualien Hsien, inside Taroko, *E. Matsuda in 1918* (TAIF, TI); Hualien Hsien, from Karen to Goken-yama-ako, *T. Namba et al. 2215* (TI); Ilan Hsien, Kizan, Kwan-zan Pass, *S. Okamoto in 1938* (KYO); Nantou Hsien, Musha, Mt. Ali Shan, *W. R. Price 810* (K); Taichung Hsien, near Wuse, *R. R. Ream 515* (G); Nantou

Hsien, Taityu, Musya, *S. Sasaki in 1919* (TAI); Hualien Hsien, Nang-kao-shan, *S. Sasaki in 1922* (TAI); Chi-lai-shan, *S. Sasaki in 1926* (TAI); Taichung Hsien, Ma-ni-ko-an, *S. Sasaki in 1930* (TAI); Sa-la-ma-o, *S. Sasaki in 1932* (TAI); Tagiri, *S. Sasaki in 1932* (TAI); Hualien Hsien, *T. Suzuki 16137* (PE); Taichung Hsien, Huan-shan, *M. Tamura 21023* (SHIN); Taichung Hsien, Mt. Hsueh-shan, between Huan-shan & Shikayo-to-shan, *M. Tamura 21037* (SHIN, TI); Nantou Hsien, Musya-san-tinojo-onsen, *without collector 2096* (TAI); Hualien Hsien, Neng-kao-shan, *without collector in 1922* (TAI). XIZANG: Zayu Hsien, *Qinghai-Xizang Exped. 73727* (PE). YUNNAN: San-chuang, *J. Cavalerie 3781* (K); Yangpi, *Chungtien Exped. 63-4119* (KUN); Houang-li-pin, *J. M. Delavay in 1887* (P); Kan-hai-tzu, *J. M. Delavay in 1888* (A); Ta-lung-tan, *J. M. Delavay 4194* (K, MO, P, TNS, W); region of Ping-tchouan, *F. Ducloux 7113* (P); Atungtze, *K. M. Feng 23615* (KUN); E flank, Lichiang Range, *G. Forrest 2754* (E); SE of Tengyueh, *G. Forrest 8331* (E, K); Mekong-Salwin divide, *G. Forrest 13254* (E); near Tengyueh, *G. Forrest 24798* (E, G, K, NY, US); Chungtien, *H. Handel-Mazzetti 4813* (W); Tse-kou, *Monbeig 101* (E, K), *1912* (P), *R. P. Soulie 1188* (G, P), *R. P. Soulie s.n.* (BM, DS, E, G, K, P, US); Kunming, *Stat. Kunming 55222* (NAS); Che-tse-lo, *H. T. Tsai 58483* (A, PE); Weipo Shan, Menghwa, *Y. Tsiang 11904* (NAS); Weixi Hsien, *C. W. Wang 67929* (A, NAS, TAI), *88223* (NAS), *68223* (A, PE); Degen Hsien, *C. W. Wang 69110* (PE); Huan-fu-ping, Atuntze, *C. W. Wang 69110* (A, NAS); Shun-ning, Wumulung, *T. T. Yü 16582* (A, E); Chenkang, Montung, *T. T. Yü 17475* (A, E). ZHEJIANG: Hsi-tian-mu Shan, *S. S. Chien 661* (NAS); Tianmu Shan, *H. C. Chu 365* (NAS), *S. Y. Ho in 1957* (NAS), *Y. Y. Ho 25339, 25494, 25576* (NAS), *W. Y. Hsia 202* (PE), *K. C. Kuan 75467* (PE); Hsi-tian-mu-shan, *Y. W. Law 1166* (K, NAS, PE, TAI); Tian-mu-shan, *H. C. Liu & W. C. Cheng 5034* (K), *T. N. Liou 6594* (PE); Hsi-tian-mu-shan, *H. Migo in 1930* (NAS), *H. Migro in 1935* (TI). "MANCHURIA": around Ichi-si-da-gou, *V. Komarov in 1897* (BM, LE, P); around Pada-gou, *V. Komarov in 1897* (G, LD, NY); Mukden, near Imperial Tombs, *D. Litvinov 3173* (G, NY); Popiet, *C. Maximowicz in 1860* (K); "Port May," *C. Maximowicz in 1860* (BM, K, L, NY, P, S, US, W); Utsentientze, *B. V. Skvortsov in 1927* (G); Anto Prov., Soukakou, *I. Yamatsuta 947* (TNS). LOCALITIES UNKNOWN: Ying-ning, Pai-t'a, *L. Chavet 418* (W); Mt. Miao-wang-shan, Mt. No-mi-shan, *Fr. Hugh in 1899* (BM); plain of Hua kia Hsien, *Fr. Hugh in 1898* (BM); Sokako, *M. Kitagawa in 1926* (TI); "Western China," *E. H. Wilson 4461* (A, K); Kosei-sho, Kyuko-fu, Mt. Rozan, *without collector 81* (TI).

INDIA. Dalhousie, *C. B. Clarke 22842, 22592* (K), *23029* (BM); Chamba State, Pangi, below Sanch, *J. F. Duthie in 1899* (CAS); near Simla, *Jacquemont herb. 2408* (K); Punjab, Dalhousie, *W. Koelz 8880* (NA); Di Chu (also at Rima), *F. Kingdon-Ward 20043* (BM, E); NW Himalaya, 7–8,000 ft, *T. Thomson s.n.* (GOET, K, L). KASHMIR: Chamba State, Bassued Forest, Chanju Valley, *J. H. Lace 1981* (DS, E); Tangmarg, *R. R. Stewart 10568* (NY, PENN); Palgam, Liddar Valley, *J. F. Duthie 13168* (BM); vicinity of Palgam, on E Liddar road, 27 road mi. N of Islamabad, *F. G. Dickason 762* (MICH); in central mountains (Pir Parg, Gulmay, etc.), *J. R. Drummond 15042* (E); Palgam, *C. B. Clarke 31143* (K), *R. R. Stewart 9233* (NA), *Stewart 21600a* (K, NY, US).

JAPAN. HOKKAIDO. Sapporo, *S. Arimoto in 1903* (G), *Arimoto in 1902* (MO); Rishiri Island, Higashi-rishiri-cho, Omobetsu-zawa, *D. E. Boufford & E. W. Wood 19822* (CM, KYO, MHA, MO); Hidaka Shicho, Samani-gun, Samani-cho, Okada, *D. E. Boufford & E. W. Wood 19699* (BM, CM, E, G, K, KYO, LD, MHA, MO, NCU, P, PE, SHIN); Ishikari Shicho, Sapporo, Mt. Maru-yama, *D. E. Boufford & E. W. Wood 19631* (KYO, MO); Sapporo, Mt. Teine-yama (CM, MHA, MO); Kawakami Shicho, hwy 40 just WNW of Osashima at the border of Nakagawa-cho, *D. E. Boufford & E. W. Wood 19831* (CM, KYO, MO); Otaru, *U. Faurie 1183* (G, MO), *1189* (P), *2905* (P); Rebun-shiri, *U. Faurie 2628* (G, P); vicinity of Junsainuma, *U. Faurie 6307* (BM); forests of Kamikotan, *U. Faurie 6311* (KYO); Ishikari Shicho, Mt. Moiwa, *Fujita et al. in 1928* (SAPA); Hakodate, *F. C. Greatrex 382* (SAPA); Sapporo, Mt. Maru-yama, *M. Hara in 1943* (TI); Sapporo, *S. Hori in 1885* (MAK); Mt. Iyozankei-tengu, *K. Ito in 1969* (SAPA); Oshima, Fukuyama, *T. Kawakami in 1892* (SAPA); Rishiri Island, Mt. Rishiri, *T. Kawakami in 1899* (SAPA), *G. Koidzumi 32* (KYO); Nopporo, *Y. Kudo in 1915* (TUS); Rishiri Island, Oshidomari, *T. Makino in 1903* (MAK 6903); Iburi-gun, Lake Toya-ko, *T. Makino s.n.* (MAK 6908); Mt. Raiden, *A. Masuda in 1967* (SAPA); Uoiwa, *J. Matsumura in 1899* (TI); Hakodate, *C. Maximowicz in 1861* (BM, G, K, LE, P); Mt. Horoiwa, Lake Saroma-ko, *T. Misumi in 1953* (SAPA); Sapporo, *K. Miyabe in 1891* (MO); Zenibako, Ohirobeshi, *K. Miyabe in 1890* (SAPA); Oshima, Sawara, *K. Miyabe in 1890* (SAPA); Sorachi, Sorachibuto, *K. Miyabe in 1891* (SAPA); Soumbetsu, *K. Miyabe & M. Tatewaki in 1925* (SAPA); Oshima, Ishizaki, *K. Miyabe & Y. Tokubuchi in 1890* (SAPA); Ishikari, Jozankei, *H. Muramatsu in 1928* (TI); Kitami, Rubeshibe-cho, Tokoro-gun, *G. Murata & Y. Momotani in 1955* (KYO); Nemuro, Akeshi, *S. Okamoto 963* (KYO); Tokachi, Dekubetsu, *S. Okamoto in 1955* (KYO); Mombetsu-gun, Takinowe, Penke, *S. Okamoto in 1952* (KYO); Rishiri Island, *S. Okamoto 1725* (KYO); Kitami, *S. Okamoto in 1958* (KYO); Tokachi, Kami-ashi-yori, *S. Okamoto in 1955* (KYO); Ishikari, Mt. Moiwa, *T. Sakamura in 1912* (TAI); Biei to Matsuyama, *K. Tagashi in 1918* (SAPA); Shiribeshi, Zenibako, *Takee & Murayama in 1931* (SAPA);

Kushiro, Lake Kutcharo, *M. Tatewaki in 1933* (SAPA); Sapporo, *E. Tokubuchi in 1887* (G, NY); Oshima, Junsainuma, *Y. Tokubuchi in 1888* (SAPA); Shiribeshi, Yoichi, *I. Yamamoto 4248, 4471* (KYO); Akkeshi, near Rinkaijikenjo, *T. Yamanaka in 1936* (SAPA); beside Lake Akkeshi, *T. Yamanaka in 1936* (SAPA); Mt. Teine-yama, *H. Yanagirawe in 1915* (SAPA); Sapporo, *R. Yatabe 1882* (G, TI), *Class of '80 in 1978* (SAPA), *Class of '27 in 1927* (SAPA). HONSHU. AICHI PREFECTURE: Tomiyama-mura, Ichibara, *K. Torii in 1954* (TNS); Mikawa, Mt. Ishimaki, *T. Tsunekawa in 1941* (TNS). AKITA PREFECTURE: Kazuno-gun, Shihei-mura, *S. Kurosawa in 1951* (TI); Oga Peninsula, Monzen, *R. Mochizuki 2110* (KANA); Mt. Moriyoshi, *H. Muramatsu in 1931* (TI); Yokote, Masuda-machi, *K. Yushun in 1905* (NY). AOMORI PREFECTURE: plains of Aomori, village of Takata, *U. Faurie 1124* (MO, P); Shimokita Peninsula, Mt. Osore-yama, *M. Mizushima 15205* (MAK, S). CHIBA PREFECTURE: Kimitsu-gun, Kameyama-mura, *M. Furuse in 1962* (A); Ninomiya, Tsudanuma (TNS 103100). FUKUSHIMA PREFECTURE: Mt. Iitomi-yama, *R. Endo in 1913* (TUS); Mt. Azuma, Hibara Pass, *G. Koidzumi s.n.* (TI); Kita-aizu-gun, Wakamatsu city, from Agaiyachi to Nababashi, *S. Kurosawa in 1957* (TI); Yumoto, *J. Matsumura in 1978* (TI); Numayama Pass, *G. Nakahara* (MAK 6906); Minami-aizu-gun, *J. Ohwi & M. Tagawa 462, 493, 596* (KYO); Aizu, Numayama Pass (MAK 117708). GIFU-NAGANO PREFECTURES: Mt. Norikura, *U. Faurie 6680* (BM, KYO, P). GUNMA PREFECTURE: Maruike Lake, *T. Makino in 1930 MAK 6917* (KAG, KYO, MAK, S); Tano-gun, Nakasato-mura, Nakasato, *T. Masahisa in 1957* (TNS). HIROSHIMA PREFECTURE: Nanbarakyo Gorge, *T. Makino in 1928 MAK 7053* (KANA, MAK, S). HYOGO PREFECTURE: Yabu-gun, Oya-cho, Ikada, *D. E. Boufford et al. 19575* (CM, KYO, MHA, MICH, MO, NCU, S); Mikata-gun, Onsen-cho, Kiri-taki waterfall, *D. E. Boufford et al. 19597* (CM, KYO, MHA); Taki-gun, Tannan, Mt. Ryusoji, *S. Hosomi 8837* (KYO); Mayasan, Rokukosan no uchi, *Ishikawa in 1937* (TAI); Sakanotani, Government Forest near Tokura, *T. Kodama 12446* (TNS); Mikata-gun, Onsen-cho, Kiri-taki waterfall, *G. Murata 20694* (KYO); Asago-cho, SW of Nii, Toji, Hashigatani, *M. Tagawa 7061* (KYO); Kamaguchi-mura, Myoken, Awaji Island, *8 August* (TI). IBARAGI PREFECTURE: Mt. Yamigo, *S. Masatomo in 1962* (TNS); Higashiibaragi-gun, Nagaoka-mura, *K. Tsurumachi in 1916* (TNS); Mito city (MAK 6907); Tsuchiura (MAK 117709). IWATE PREFECTURE: Hiramiwa-toge, *S. Kitamura in 1965* (KYO); Mt. Hayachine, Shimohei-hien-uki-gun, *T. Makino in 1928 MAK 6915* (MAK, S). KANAGAWA PREFECTURE: Tsukui-gun, Mt. Shiro-yama, *S. Kobayashi in 1955* (S). KYOTO PREFECTURE: cultivated in Tokyo Univ. Bot. Gard., *S. Kawagoe in 1909* (KAG). MIYAGI PREFECTURE: Oni-kubi, *K. Hosoi in 1949* (KANA); Mt. Zao, *A. Kimura & S. Sugaya in 1953* (TUS); Mt. Fubo, Namari-zawa, *K. Sohma 1531* (KYO, MO, TUS); Ishinomaki city, Fudosawa (MAK 117707). NARA PREFECTURE: Mt. Karakasa-zan, *E. Kitagawa 2* (TNS). NAGANO PREFECTURE: Suwa-gun, Okaya-shi, Yoko-kawa-dani, *D. E. Boufford et al. 19623* (CM, KYO, MO); Minamisaku-gun, Mt. Goza, Yamaguchi-michi, *H. Hara in 1958* (TI); Minamisaku-gun, Kawakami-mura, en route from Senjogahara to Mt. Mikuni-yama, *M. Hotta in 1958* (KYO); Shimotakai-gun, Sakai-mura, Kitanogami-jinja, *H. Kanai in 1962* (TI); Mt. Taro, Ueda, *S. Mochizuki 128* (SHIN); Susuwatari-kue, *S. Momose in 1933* (TI); Ukawairi, from Susawatari to Higashisawaguchi, *S. Momose in 1934* (TI); Mt. Hachibuse, *S. Momose in 1936* (TI); Todai, Kamiina-gun, Miwa-mura, *G. Murata 8004* (KYO); Ooshika-mura, Mt. Odaka, *M. Muramatsu 1508* (TNS); Ooshika-mura, Tokokuchi-yama, *M. Muramatsu 1903* (TNS); Kizawa-mura, Nishisawado, *M. Muramatsu 2627* (TNS); Kami-ina-gun, Todai, *J. Ohwi in 1929* (KYO); Ii-yama, *T. Saito in 1906* (MAK); Minamisaku-gun, Nakagome-cho, Kuroda, *K. Sato 154* (TI); Kita-aiki-mura, Mt. Goza, *K. Sato 607* (TI); Chiisata-gun, Kakuma Valley at the foot of Mt. Eboshi, *T. Shimizu 19721* (SHIN); Yokokawadani Valley, Okaya, *T. Shimizu 25817* (SHIN); Yakeyamazawa, Utsukushigahara, *S. Suzuki 492* (K); Shimoina-gun, Kisawa-mura, Toyama-gawa, *Yamasaki et al. in 1954* (TI); near Komoro city, Mt. Nonobiki (MAK 117713); Mt. Tadeshima (MAK 117714); Chiisata-gun, Nagata-cho, Honzawa (MAK 117716). NIIGATA PREFECTURE: Mt. Kurochima, *T. Ajime 4313* (KANA); foot of Mt. Yosen, *U. Faurie 212* (P); Sado Island, Ikawa, Tasha, *Y. Ikeyama 46402* (KANA); Sado Island, Ishina, *F. Maekawa in 1933* (TI); Sado Island, *T. Makino in 1933 MAK 6918* (KAG, MAK, S); Mt. Todaramine, *G. Murata 6736* (KYO); Nishikubiki-gun, Odaki-mura, *S. Uchikawa in 1953* (TNS); Higashikanbara-gun, Tsugawa, *T. Yamazaki* (TI); Itoigawa city, Mt. Myojo (KANA 085749). OKAYAMA PREFECTURE: Maniwa-gun, Katsuyama-cho, Kanba waterfall, *T. Shimizu in 1958* (KYO). OSAKA PREFECTURE: Mt. Iwawaki, *M. Tagawa 3309* (TNS). SAITAMA PREFECTURE: Okutama, Korikawa, *H. Kanai 1817* (TI); Chichibu city, *T. Makino in 1920* (MAK); Inuma-gun, Naguri-mura, Shiraiwa, *H. Ohashi et al. in 1975* (TI). SHIGA PREFECTURE: Kanzaki-gun, Yama-no-ue village, Ainotani, *T. Hashimoto in 1932* (KYO). SHIZUOKA PREFECTURE: Akaishi Mts., Mt. Toyoguchi, *Furusawa & Kuraishi in 1953* (TI); Izu Peninsula, Kamo-gun, Nando-mura, *Y. Kimura in 1943* (TI); Akaishi Mts., Oshika-mura, Koshibu-gawa, *H. Matsuda in 1953* (TI); Owigawa-joryu, Nakano-yado, *H. Matsuda in 1954* (TI); Owi-gawa-joryu, Tokusa, *H. Matsuda in 1954* (TI); Enshu Senzu Government Forest, near Hiryuubashi office, *T. Satow & Y. Hayashi 7827* (TNS). TOKYO PREFECTURE: Mt. Takao, *M. Honda in 1925* (TI); Mt. Kariyose, *M. Honda in 1929* (TI); Musashi, Nishigahara, *T. Kagasawa in 1885* (TNS); Mt. Takao, *Y. Kobayashi in 1930* (TI), *Y. Komori 566* (TI); Yoyogi in Tokyo, *T. Makino in 1900 MAK 6912* (MAK, S); Dokan-yama in Tokyo, *T. Makino in 1900 MAK 6913* (S), *MAK 6910, 6916, 117711* (MAK); Mt. Kariyose,

T. Makino in 1930 MAK 6919 (KAG, MAK); Waseda, *S. Matsuda in 1891* (KYO); Zoshigaya, *S. Matsuda in 1900* (KYO); Nishitama-gun, Mt. Minoto, *M. Mizushima 10033* (UC); Tokyo, *H. Sakurai in 1907* (E); Dokan-yama, *K. Watanabe in 1888* (G); Nishitama-gun, Hikawa-mura, Nippara, *T. Yamazaki in 1947* (TI); Ueno, *R. Yatabe & J. Matsumura in 1878* (TI); Mt. Takao (MAK 6905); Uchiai, *20 August 1910* (LD); Yoyogi, Shibuya-ku (MAK 117710), *23 September 1911* (S). TOYAMA PREFECTURE: Tateyama, Ueno-taki, *T. Ichimura 1440* (KANA); Shimo-shinkawa-gun, Miyazaki-mura, Miyazaki, *H. Kanai in 1958* (TI); Higashi-tonami-gun, Taira village, Ainokura, *Mimuto, Sugaru & Mori 12703* (KYO). YAMAGATA PREFECTURE: Higashine city, Makino, *D. E. Boufford & E. W. Wood 19880* (BM, CM, E, K, KYO, MHA, MO, PE); Owisawa, Naka-mura, Yudono-jinja, *H. Hara in 1959* (TI); Higashi-murayama-gun, near Yamadera Station, *H. Kanai in 1959* (TI); Yamagata city, near Kabutoiwa, interior of Yamadera, *H. Ohba 718033* (MAK, MO); Uzen, Sanbonginuma, *S. Okayama in 1931* (TNS). YAMAGUCHI PREFECTURE: Nagato, Abu-gun, Koshigahama, Kasayama, *J. Nikai 389* (TNS); Abu-gun, Higashiwaku-mura, Aza-koshigahama, Mt. Kasayama, *S. Nishina 389* (TI). YAMANASHI PREFECTURE: Nakakoma-gun, Ashiyasu-mura, Yashajin-toge, *M. Furuse 19553* (S); Minamitsuru-gun, Nakano-mura, *M. Furuse in 1959* (A); foot of Mt. Fuji-san, *K. Hiyama 4003* (TNS); Mt. Kuro-take, *K. Hiyama in 1933* (TNS); Mt. Amago, Shimobe-onsen, Yuno-oku, *H. Kanai in 1955* (TI); Nishiyatsushiro-gun, Okachi-mura, Tsubakizori, *H. Kanai in 1957* (TI); NNE part of Mt. Fuji-san, Fujiyoshida Sengen-jinja, *G. Murata et al. 33837* (KYO, MO); Nakakoma-gun, Ashiyasu-mura, *T. Yamazaka in 1954* (TI). SHIKOKU. KOCHI PREFECTURE: Hata-gun, Taisho-cho, Shimotsui, *Y. Kanematsu s.n.* (MAK 117717); Nano-kawa, *27 July 1892* (G). TOKUSHIMA PREFECTURE: Mt. Tsurugi, *T. Makino in 1909* (MAK 6909); between Sugeoi and Ochiai, Higashiiyama-mura, *G. Murata in 1954* (KYO); Mt. Takane, *Z. Tashiro in 1935* (KYO); Shimona-mura, *R. Yatabe in 1888* (TI). KYUSHU. KUMAMOTO PREFECTURE: Mt. Ohira, *K. Mayebara 5386* (TI). OITA PREFECTURE: Beppu, *Z. Tashiro in 1936* (KYO); Hita-gun, Amekata, *K. Hashimoto in 1927* (MAK).

KOREA, NORTH. Heian-hokudo, Mt. Myoko, *G. Koidzumi in 1935* (KYO); near the town of Ludzu, *V. Komarov in 1897* (LE); around Tauanin-dou, Yalu R., *V. Komarov 1140* (W); Sei-sui-ra, *J. Ohwi in 1930* (KYO); Heinan-kakigai, *17 July 1916* (TI).

KOREA, SOUTH. Chongju, Chungchong-pukto, *I. C. Chung 9743* (MICH); Toku-san, Keisho-nando, *T. Mori 241* (TI); Utsuryo-to Island, *T. Nakai 4462* (TI); Mt. Kongo, Gunsenkyo, *T. Nakai 5688* (TI); Kokai, O-aoshima, *T. Nakai 13300* (TI); Chuhoku, Zokuri-san, Jokan-ando, *T. Nakai 15081* (TI); Mt. Tii, *S. Okamoto 27 July 1937* (KYO, TNS), *4 August 1937, 27 August 1937* (KYO); Kogen-do, Mt. Kongo, *T. Uchiyama in 1902* (TI).

KOREA, LOCALITIES UNKNOWN: Kim-o-san, *C. I. Chung 9936* (MICH); Hoang-hei-to, *U. Faurie 655* (BM, KYO, P); See Chun Dong, *G. Mills in 1910* (UC).

A single sheet with only "Mongolia," *A. David 1889* (P).

NEPAL. NW of Jumla, Chanki, *W. R. Sykes & L. H. J. Williams 5078* (BM, E, UPS); E of Jumla, Lorpa, *O. Polunin et al. 4958* (BM, E).

PAKISTAN. HAZARA DISTRICT: 1 mi. from Kawai on way to Shogran, *S. Abedin & M. Qaiser 8780* (KUH); Murree Hills, Upper Topa, *J. H. Barbour in 1920* (BM); Hazara, *J. F. Duthie 21335* (W); Rawalpindi, Murree, *Fleming 345* (K); Kagan Valley, Kamalban, *A. H. Khan in 1927* (UC); Murree Hills, *Nasir & R. R. Stewart 29161* (RAW); Murree Hills, Patriata, *M. A. Siddigi & Y. Nasir 6076* (RAW); Changla Gali, Murree Hills, *R. R. Stewart in 1948* (K, PH); Nathia Gali, *R. R. Stewart 28716* (RAW, SMU); Thandiaru, *R. R. Stewart 27747* (G). SWAT STATE: Mt. W of Swat R. above Bahrein, *R. J. Rodin 5558* (RAW, UC, US); Bahrein, *R. R. Stewart 24479* (BM, NY, W); W Himalaya, *J. F. Duthie in 1899* (POM, UC).

Circaea cordata is one of the most distinct species of *Circaea* and has been the source of little confusion since its recognition by Royle in 1834. The dense, usually spreading pubescence, flowers clustered at the apex of the raceme, short pedicels in flower and fruit, distinctive shape and close spacing of the bilocular, 2-seeded fruits, and the nectary wholly included within the floral tube set *C. cordata* off from all other species of the genus. The absence of an exserted nectary is shared only with C. *glabrescens* among species bearing bilocular, 2-seeded fruits.

Plants with the leaf bases rounded rather than cordate occur sporadically throughout the range of the species but with a higher incidence of occurrence in northwestern India, Kashmir, and Pakistan. A few examples of these plants are

J. Lace in 1921 (E), *J. Barbour in 1920* (BM), *E. Wilson 1545* (NY), *Y. Tsiang 5804* (S), and *K. Chow 131* (A). Variation in the shape of the leaf base may occur within a population, or even on the same plant as exhibited by *Handel-Mazzetti 12317* (E) from Hunan which has cuneate, rounded, truncate, and subcordate bases. Pubescence is also variable. A few specimens from China and Pakistan have only sparse pubescence on the stem and the long straight hairs are greatly reduced in number. The numerous intergrading populations between these and more typically pubescent plants rule out the possibility of formal taxonomic recognition.

Circaea cordata prefers drier habitats throughout its range than any of the other species of the genus. It is often found on dry slopes and on drained, raised areas in alluvial forests.

2. Circaea glabrescens (Pamp.) Hand.-Mazz., Symb. Sin. 7: 604. 1933.—FIG. 5.

Circaea cordata Royle var. *glabrescens* Pamp., in Nuovo Giorn. Bot. Ital. n.s. 17: 677. 1910.

Plants erect or decumbent at the base, 1.2–8 dm tall, simple or occasionally branched below the inflorescence, forming non-tuberous rhizomes that give rise to the following year's plants from their tips. Plants pubescent, rarely glabrous. The stem with short, 0.1–0.3 mm long, soft, falcately recurved hairs; the petioles with short, ca. 0.2 mm long, upwardly pointing, soft, falcate hairs which ± continue along the main veins on the lower, and occasionally also on the upper, surface of the leaf, the leaf also with longer, ca. 0.5 mm long, straight, slightly curved or falcate hairs evenly and sparsely distributed over both surfaces, leaf margins with falcate and straight hairs intermixed. Stem green, nodes brownish or those of the inflorescence sometimes reddish purple. Median leaves to those just above the middle of the stem the largest, 3.7–8(–11) cm long, 1.8–5 cm wide. Leaves becoming gradually reduced in size upward from the middle of the stem and then abruptly reduced just below the inflorescence and ultimately bractlike and remaining opposite, or occasionally one or two bracts above these alternate. Leaves gradually reduced in size downward from the middle of the stem. Leaves narrowly to broadly ovate, acuminate to short acuminate, rounded or, very rarely, subcordate at the base, denticulate. Petioles terete, 0.5–4.5(–5.5) cm long, occasionally with reduced branches arising in the axils. Inflorescence glabrous, very rarely sparsely glandular pubescent, terminal on the main stem and rarely at the tips of the uppermost axillary branches, a simple raceme or, more commonly, branched at the base, when branched, the lowest branches opposite and subtended by brachts, the uppermost branches alternate, with, or more commonly, without subtending bracts. Terminal raceme from the uppermost reduced leaf or leaflike bract, or from the uppermost branch at the base of the raceme, 2–5 cm long at initiation of flowering, to 18 cm long at cessation of flowering; lateral racemes ca. 2–3 cm long at initiation of flowering, to 12 cm long at cessation of flowering, subequal length on the same plant. Flowering pedicels 1.3–2.5(–3.3) mm long, perpendicular to the axis of the raceme, glabrous, subtended by a setaceous bracteole, 0.1–0.5 mm long. Fruiting pedicels 2.3–4(–5.5) mm long. Buds glabrous or, more commonly, pubescent, especially at the apex, with a few long, straight to slightly bent hairs, 0.4–0.5 mm long, occasionally also with short

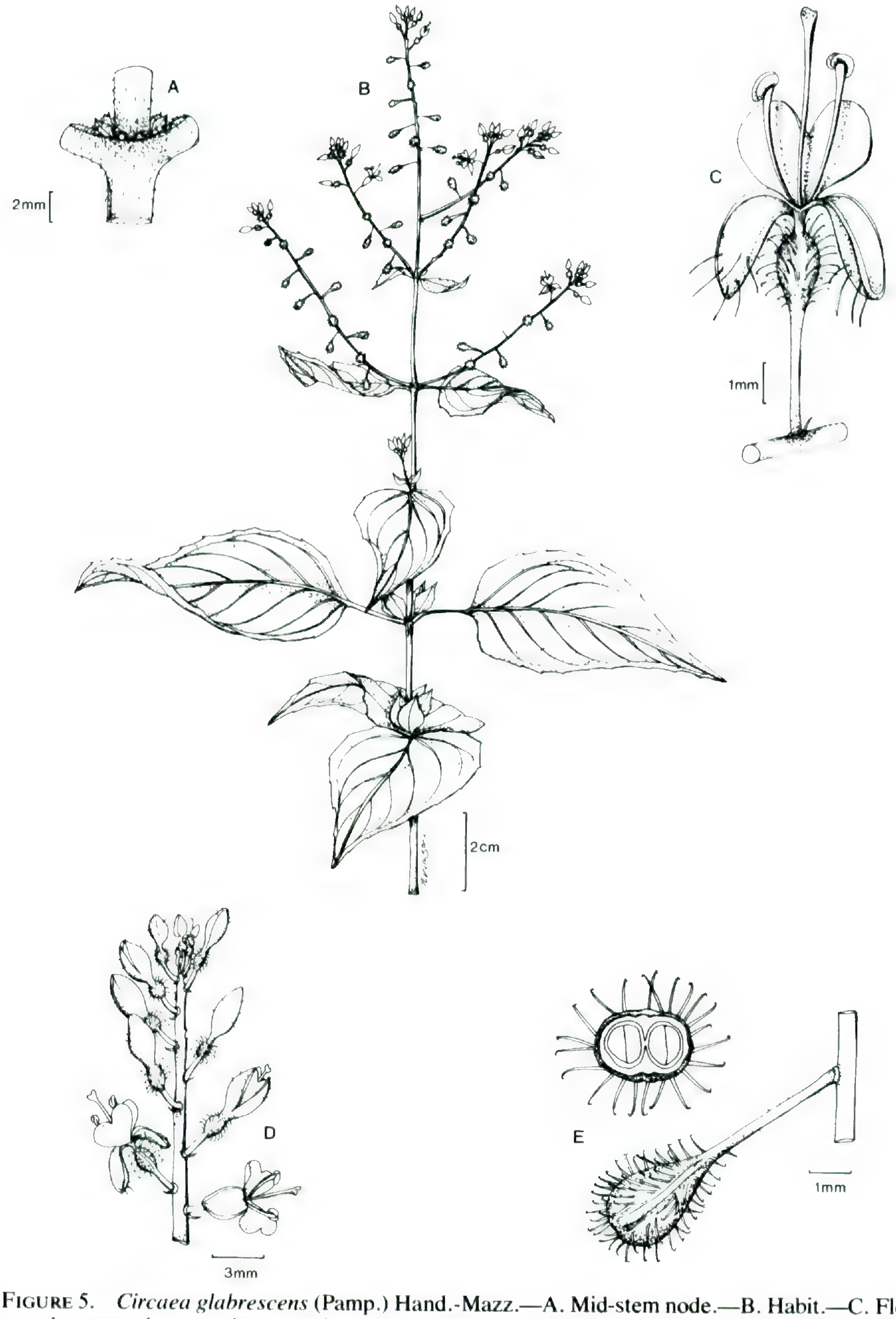


FIGURE 5. *Circaea glabrescens* (Pamp.) Hand.-Mazz.—A. Mid-stem node.—B. Habit.—C. Flower with petal removed; note absence of exserted nectary.—D. Inflorescence.—E. Fruit. From *Smith 6492* (LD, UPS).

capitate and clavate-tipped glandular hairs, 0.1–0.2 mm long; pink or pale green; slenderly elliptic to obovoid, acute or obtuse at the apex; from the summit of the ovary, 2.8–3.5(–4.5) mm long, 1.2–1.6 mm thick just prior to anthesis. Ovary 1–1.2 mm long, 0.8–1 mm thick at anthesis, elliptic to obovate in outline, pubescent

with translucent, uncinate hairs. Floral tube 0.9–1.3 mm long, 0.1–0.4 mm thick at the narrowest point, very slenderly obconic to slender funnelform. Sepals 1.8–3.3 mm long, 1.2–1.7 mm wide, glabrous or, more commonly, pubescent on the abaxial surface with hairs as on the buds, pink or greenish white; oblong to nearly ovate, rounded smoothly from above the middle to the acute or obtuse apex; reflexed in flower. Petals 1–1.9 mm long, 1.3–2.6 mm wide, wider than long, pink, oblate to broadly obovate in outline, the apex obcordate, tapering concavely or short-clawed at the base; the apical notch 0.3–0.6 mm deep, ca. ½ the length of the petal, the petal lobes broadly rounded. Stamens spreading at anthesis, shorter than the style; filaments 1.6–3.7 mm long; anthers 0.5–0.6 mm long, ca. 0.4 mm thick. Style straight, erect, 3.2–4.7 mm long, topped by an obconic to obtriangular, shallowly bilobed stigma, 0.3–0.4 mm tall, 0.3–0.5 mm thick. Nectary wholly included within the floral tube and inconspicuous. Mature fruit 2.5–3.3 mm long, 1.6–1.8 mm thick, bilocular and 2-seeded, obovoid to obpyriform, rounded at the apex, tapering smoothly to the pedicel, without ribs or sulci but with a shallow groove which represents an extension of the pedicel, densely covered with stiff, translucent, uncinate hairs ca. 0.9 mm long, except along the extension of the pedicel, and with short, capitate and clavate-tipped glandular hairs ca. 0.1 mm long. Fruiting pedicels horizontally spreading to slightly reflexed at maturity. Combined length of pedicel and mature fruit, 4.5–6(–8.5) mm long. Gametic chromosome number, $n = 11$.

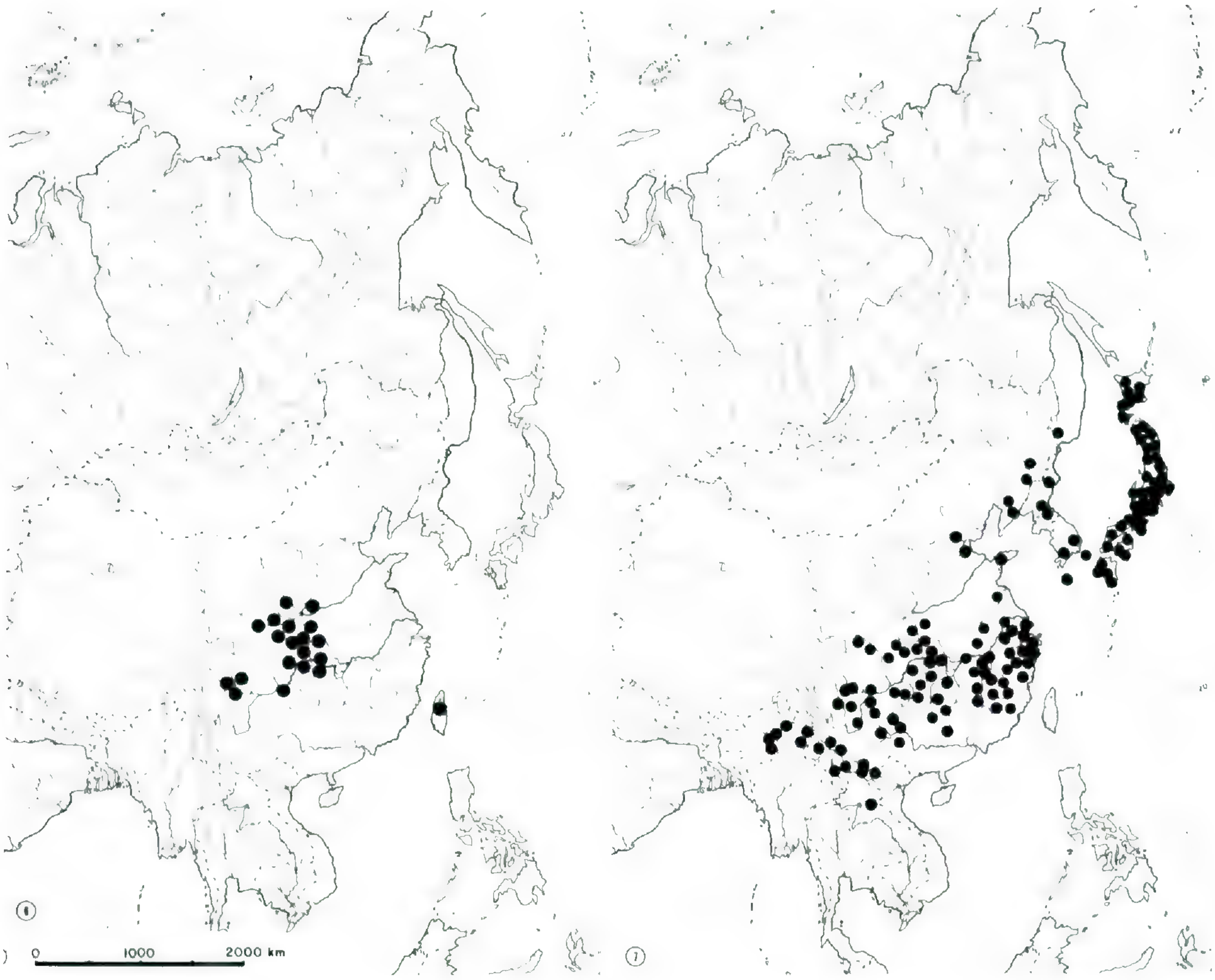
TYPE: China, Hubei, Mts. of Ch'ing-shan-chiang ("Tcin-Scian-Sien"), ca. 700 m. September 1907, *Silvestri 1571* (FI, holotype not seen. BM, DS, photographs).

Distribution (Fig. 6): Deciduous forests. Central China, from western Hubei and northern Sichuan through southern and central Shaanxi to southwestern Shanxi; southeastern Gansu; disjunct to Taiwan (one collection). From 700 to 2,500 m. Flowers, July and August.

Specimens examined:

CHINA. HENAN: Lushi Hsien, *L. C. Chen 34609* (PE); Sung Hsien, *L. C. Chen 34966* (PE); Xixia, *Henan Exped. 1164* (NAS); Lushi Hsien, *K. M. Liou 4643* (PE), *K. M. Liou 4710* (G, K, PE). HUBEI: *A. Henry 4851* (E, G, K); "Cien-shih" written on sheet, *A. Henry 6041* (K, P); Hsing-shan, *A. Henry 6498* (BM, GH, K, NY, P, US); Xingshan Hsien, *H. J. Li 83, 610* (PE); Shennongjia, *Shennongjia Exped. 1192, 11309, 20843, 21364, 21486, 31065, 31225, 32214, 32529* (all PE); Chang-yang, *E. H. Wilson 1481* (E, NY, US, W). GANSU: Tianshui Hsien, *W. Y. Hsia 5812* (PE); Tianchi Shan, *W. Y. Hsia 5955* (PE); Pingliang Hsien, *Huanghe Exped. 2067* (NAS, PE); Tianshui Hsien, *K. M. Liou 10066* (PE); Tianshui Hsien, *C. W. Wang 57, 164, 10201* (all PE); Pingliang Hsien, *T. P. Wang 13323* (PE); Pingliang, Kunlun Mt., *K. H. Yüan et al. 2067* (PE); Tianshui, *C. W. Zhang 164* (NAS). SHANXI: Yüan-chu'ü, Shui-wang-p'ing, *H. Smith 6492* (LD, UPS). SHAANXI: Zhouzhi, *S. M. Chang 30* (NAS); Foping Hsien, *K. T. Fu 4999* (PE); Hu Hsien, Cho-toe-miao, *Hugh s.n.* (BM); Ningshen Hsien, *H. W. Kung 3199* (PE); Hu Hsien, *P. C. Kuo 306, 396* (PE); Ankang Hsien, *P. Y. Li 3200* (NAS); Tsingling Mts., *E. Licent 2682* (BM, K, P, W); Taibai Shan, *T. P. Wang 1607* (PE); Shang Hsien, Hei-shan road, Yu-huang-ting, *T. P. Wang in 1952* (PE). SICHUAN: Pao-hsing Hsien, *K. L. Chu 3403* (BM), *3404* (W); Omei Hsien, *W. P. Fang 2805* (PE); Fengjie Hsien, *M. Y. Fang 24565* (NAS, PE); Fu-hsing-chen, Ch'eng-k'ou ("Tchen-keou-tin") district, *R. P. Farges 171* (E, K, MO, P); Nanchuan Hsien, *K. F. Li 62708, 63422* (PE); Baoxing Hsien, *T. P. Sung 39263* (PE); Chengkuo Hsien, *T. L. Tai 101137* (PE), *104089, 105601* (NAS, PE); Nanchuan Hsien, *J. H. Xiong 92218* (PE); Wushan Hsien, *K. H. Yang 58961* (NAS, PE); Wusi Hsien, *K. H. Yang 59404* (NAS, PE). TAIWAN: Hualien Hsien, Tai-lu-ko ("Ta-gi-li"), *S. Sasaki in 1932* (TAI 081843).

This species is by far the most local of the species of *Circaea*. The collections are from relatively widely scattered areas in central China and from a single



FIGURES 6–7.—6. Distribution of *Circaea glabrescens* (Pamp.) Hand.-Mazz.—7. Distribution of *Circaea mollis* Sieb. &. Zucc.

disjunct station in Taiwan. The specimen from Taiwan is part of a mixed collection and is mounted on the same sheet with *C. erubescens*. According to Ching-I Peng (pers. comm.), the site where it was collected in 1924 at Tai-lu-ko ("Tagi-li") has now been converted into a holiday resort and the plant may have been exterminated. Attempts to relocate *C. glabrescens* in Taiwan should still be made, however.

Circaea glabrescens bears some resemblance to *C. cordata* and *C. erubescens*. It resembles *C. erubescens* most closely in the shape and size of the fruit, so much so that it would be difficult to say to which of the two species an isolated fruit belonged. On critical examination, however, it appears that *C. glabrescens* is much more closely related to *C. cordata* than to any of the other species of the genus. Characters shared by *C. glabrescens* and *C. cordata* are: nectary wholly included within the floral tube; relatively short pedicels in flower and fruit; similarity in petal shape; and consistent presence of bracteoles. The long hairs at the apex of the buds in some populations of *C. glabrescens* are identical to the long, spreading hairs of *C. cordata*.

It has been suggested by Raven (1977) that the single collection of *Circaea glabrescens* from Taiwan might be the result of hybridization between *C. eru-*

bescens and *C. cordata*. Field and herbarium studies have shown that hybrids of that combination bear no similarity to *C. glabrescens*, and in the field living plants of *C. glabrescens* are very distinct. Raven has examined pollen from the single specimen of *C. glabrescens* from Taiwan and has noted on the sheet "pollen good." Pollen of *C. cordata* × *C. erubescens* produces 15% or less good pollen.

Circaea glabrescens has been the source of much confusion and roughly half of the plants attributable to this species have been misidentified. In addition, several collections of other species, or of hybrids, have been called *C. glabrescens*. Oddly enough, *C. erubescens* is the species with which *C. glabrescens* is most often confused, perhaps owing to similar vegetative appearance. The most characteristic feature of *C. glabrescens* is the absence of an exserted nectary, always present in *C. erubescens*. *Circaea erubescens* always has petals longer than wide, obtrullate to obovate in shape, and the apical notch one fifth or less the length of the petal. In *C. glabrescens* the petals are wider than long, oblate to broadly obovate, and the apical notch is ca. one third the length of the petal. The hybrids with which *C. glabrescens* has been confused always have the nectary exserted, at least as a low ring at the mouth of the floral tube. Once these discordant elements are removed, *C. glabrescens* shows a high degree of morphological constancy and can be recognized easily.

3. Circaea mollis Siebold & Zucc., Abh. Akad. Muench. 4: 134. 1843.—FIG. 8.

Circaea coreana H. Lév., *in* Fedde Repert. Spec. Nov. Regni Veg. 4: 226. 1907. TYPE: Korea, Hoang-kei-to, August 1906, *U. faurie 654* (BM, lectotype; KYO, isolectotype).

Circaea coreana H. Lév. var. *sinensis* H. Lév., *in* Fedde Repert. Spec. Nov. Regni Veg. 4: 226. 1907. TYPE: China, Guizhou, *J. Esquirol 647*.

Circaea lutetiana L. var. *taquetii* H. Lév., *in* Fedde Repert. Spec. Nov. Regni Veg. 7: 340. 1909. TYPE: South Korea, Cheju-do (Quelpaert Isl.), in forest of Yeng-sil, 1,000 m, 17 August 1908, *E. taquet 828*.

Erect or occasionally decumbent at the base, 2.5–15 dm tall, freely branched, especially above, with numerous axillary branches, rarely simple; forming long rhizomes without tuberous thickenings which give rise to the following year's plants from their tips. Stems pubescent, often very densely so, with soft, short, falcately recurved hairs ca. 0.2 mm long; petioles with soft, short, upwardly curved falcate hairs ca. 0.2 mm long; main veins and leaf margins with hairs as on the petioles, the interveinal areas with soft falcate hairs ca. 0.1 mm long, these occasionally lacking on the lower surface, rarely lacking on the upper; axis of the inflorescence with hairs as on the stem, 0.2–0.3 mm long, or with capitate or clavate-tipped glandular hairs 0.2–0.3 mm long, or with a combination of these or sometimes glabrous; buds, sepals and floral tube with short, ca. 0.1 mm long, soft, capitate or clavate-tipped glandular hairs, sometimes the floral tube glabrous, less frequently the buds and sepals glabrescent or glabrous. Stems green, the nodes darkened, brownish or reddish purple. Leaves horizontally spreading, the longest somewhat drooping at the tips, green, opaque; those at, or slightly above, the middle of the stem the largest, (3–)5.5–13(–16) cm long, 2–5.5 cm wide, becoming gradually reduced in size upward and eventually bractlike and opposite or alternate at the base of the inflorescence; narrowly to broadly lanceolate to narrowly ovate, smoothly tapering to slightly acuminate to the obtuse or subacute tip, narrowly to broadly cuneate, or occasionally rounded at the base, subentire

to denticulate. Petioles (0.7–)1.2–2.5(–4) cm long, sparsely to densely pubescent, with upwardly curved, falcate hairs ca. 0.2 mm long; most commonly with floriferous branches in the axils, occasionally with the lower branches reduced and nonfloriferous, very rarely without axillary floriferous branches. Inflorescence glabrous or sparsely to densely pubescent; when pubescent, with falcately recurved hairs as on the stem, 0.2–0.3 mm long, or with capitate or clavate-tipped glandular hairs 0.2–0.3 mm long, or with an admixture of the two; terminal on the main stem and at the tips of the axillary branches, the terminal raceme most commonly branched at the base, rarely simple, the racemes at the tips of the axillary branches usually simple; branches at the base of the terminal raceme opposite or the uppermost alternate, subtended by reduced leaves or leaflike bracts; the terminal raceme, from the uppermost leaves or leaflike bracts, 1.5–4 cm long at initiation of flowering, to ca. 20 cm long at cessation of flowering, the lateral racemes 1–3 cm long at initiation of flowering to ca. 15 cm long at cessation of flowering, subequal in length on the same plant. Flowering pedicels 1.5–3(–3.3) mm long, perpendicular to the axis of the raceme, without, rarely with, a minute, setaceous bracteole, 0.1–0.3 mm long, at the base; glabrous, or more commonly pubescent with capitate or clavate-tipped glandular hairs, 0.1–0.2 mm long. Fruiting pedicels 2.3–3.2(–4.2) mm long. Buds glabrous or pubescent with short, somewhat crisped, glandular hairs ca. 0.1 mm long or with straight, capitate and clavate-tipped glandular hairs 0.1–0.2 mm long; green, ovate to broadly so to oblong or obovate in outline, smoothly rounded or very short acuminate to the obtuse or minutely mammiform apex; (2.2–)2.5–3.2(–4.2) mm long, (0.9–)1.1–1.4(–1.8) mm thick just prior to anthesis. Ovary (1–)1.2–1.8 mm long, 0.8–1.5 mm thick at anthesis, pyriform to globose, densely covered with soft, translucent, uncinate hairs. Floral tube 0.5–0.8(–1) mm long, 0.2–0.3 mm thick at the narrowest point, obconic to funnelform, glabrous or occasionally pubescent, with short, capitate and clavate-tipped glandular hairs ca. 0.1 mm long. Sepals 1.6–2.4(–2.9) mm long, 1–1.5 mm wide, abruptly short acuminate to the obtuse or minutely mammiform-tipped apex, glabrous or occasionally pubescent abaxially, with short capitate and clavate-tipped glandular hairs ca. 0.1 mm long; pale green or whitish; divergently spreading or somewhat reflexed in flower. Petals (0.7–)1–1.8 mm long, (1–)1.4–2.6 mm wide, white, broader than long, rarely longer than broad, broadly to very broadly depressed obovate in outline, occasionally short-clawed; the apical notch 0.2–0.5(–0.8) mm long, ¼–½ the length of the petal. Stamens normally spreading at anthesis, shorter than or occasionally equal to, rarely longer than, the style; filaments 0.8–1.8(–2.1) mm long; anthers 0.5–0.7 mm long, 0.3–0.6 mm thick. Style straight or slightly drooping, 1.8–2.9(–3.9) mm long, topped by a narrow, transversely oblong or depressed obtriangular, prominently bilobed stigma, 0.3–0.4 mm tall, 0.5–0.8 mm thick. Nectar secreting disc conspicuous and exserted above the floral tube, 0.2–0.4 mm tall, 0.4–0.5 mm thick, cylindrical. Mature fruit 2.6–3.5 mm long, (2–)2.4–3.2 mm thick, very broadly pyriform to globose, rarely narrowly pyriform, truncate to slightly rounded at the apex, ultimately tapering concavely and obliquely to the pedicel; bilocular and 2-seeded, with prominent ribs and deep sulci, densely covered with stiff, translucent, uncinate hairs, 0.5–0.7(–1) mm long, these commonly restricted to the summit of the ribs, also with short, capitate and clavate-tipped glandular hairs ca. 0.1 mm

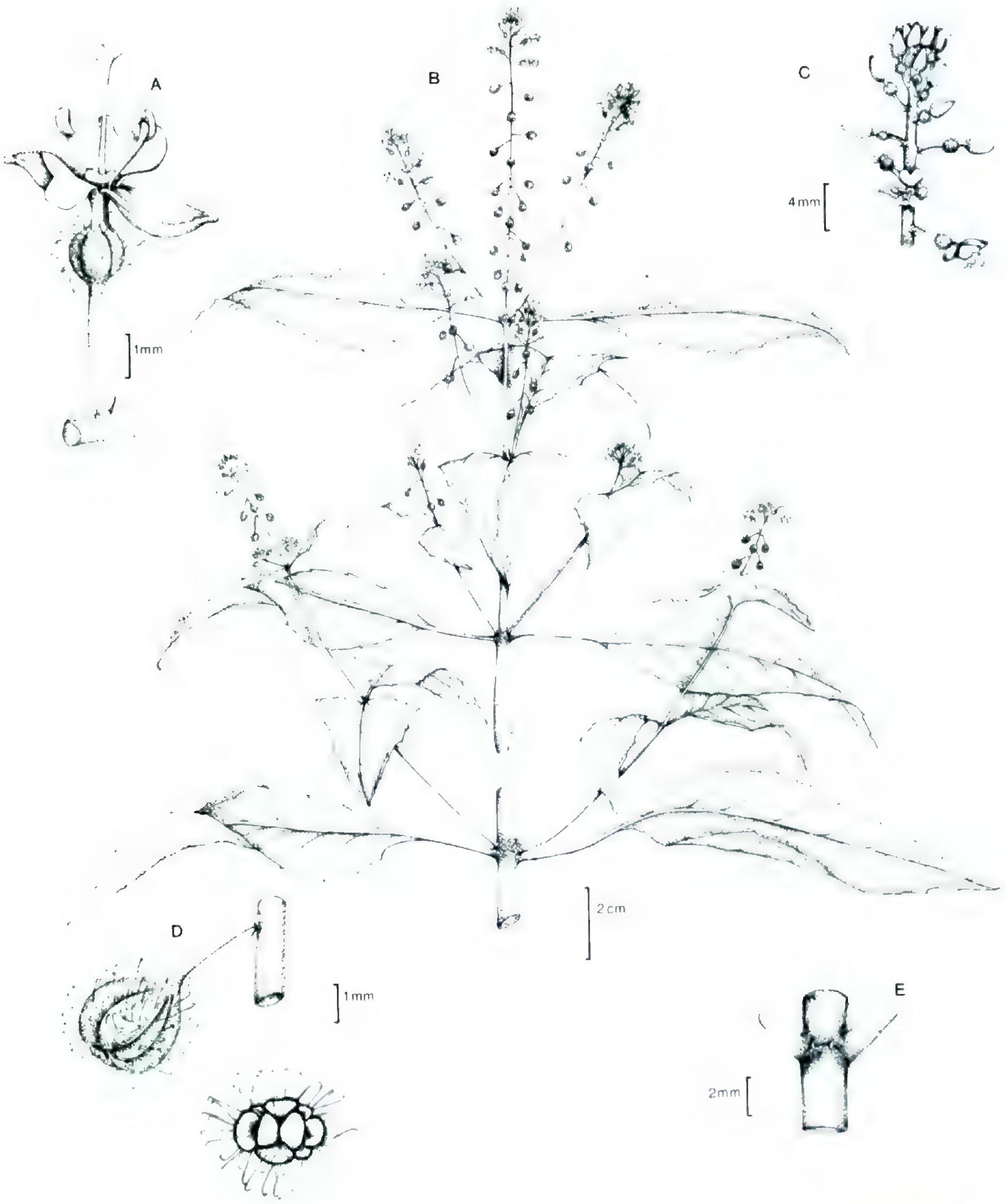


FIGURE 8. *Circaea mollis* Sieb. & Zucc.—A. Flower; note exserted nectary.—B. Mid and upper flowering stem.—C. Inflorescence.—D. Fruit.—E. Upper node of stem. From *Boufford & Wood 19553* (KYO, MHA, MO, PE).

long. Fruiting pedicel reflexed, often sharply so, at maturity. Combined length of pedicel and mature fruit, 5–7 mm long. Gametic chromosome number, $n = 11$.

TYPE: Japan ("Nipponia"), *P. Siebold* (L, lectotype. P, photograph; L, 2 sheets isolectotypes).

Distribution (Fig. 7): Cool to warm temperate deciduous forests. Japan, from central Hokkaido southward to southern Kyushu; South Korea, including Cheju-do (Quelpaert Island); locally in northeastern China and southeastern U.S.S.R.,

and then more commonly near the coast from Beijing to south-central China, then westward across southern China to the northern mountainous areas of Vietnam, Cambodia, Laos, Burma, and easternmost Assam, India. Near sea level to ca. 1,700 m. Flowers mid-July to early September, sporadically to mid-September.

Representative specimens examined:

U.S.S.R.

RUSSIAN S.F.S.R. A specimen from Sachalin, Yuzhnosakhalinsk ("Toyohara"), *S. Akiyama in 1933* (KANA), may be this species. Skvortsov (1979) cites two collections from the Soviet Union, both from the vicinity of Lake Hanka in the extreme southeastern part of the Soviet mainland.

ASIA

BURMA. Hills N of Geawgaw, *G. Forrest 24829* (E); Bhamo, *A. Huk in 1892* (K).

CHINA. ANHUI: Jurhua, *Exped. Anhui 5361* (NAS); Hai-Wei Monastery, *Y. L. Keng 2641* (NAS); Huo Mt., *Stat. Bot. Est. China 6755* (NAS); Guangse, *without collector 2931* (NAS). FUJIAN: Nanjing Hsien, *Amoy Univ. Exped. 1159* (PE); Shouning Hsien, *R. C. Ching 2276* (A, E, S, UC, US, W); Jianning Hsien, *Z. Y. Li 7901* (PE); Liancheng Hsien, *Y. Ling 3945* (PE); Wuyi Shan, *C. P. Tsien 400769* (PE); Lianchung Hsien, *D. S. Wang 1065* (PE). GANSU: Wen Hsien, *Z. Y. Chang 14620* (PE). GUANGXI: Damiao, *S. C. Chan 15220, 16871* (NAS), *15379* (NAS, PE); Linyen, Tsinglung Shan, *R. C. Ching 6879* (A, NAS, NY, S, W); Lungsheng Hsien, *Guangfu Exped. 1066* (PE); Lingluo, *S. K. Lau 18700* (A, NAS); Lingyun Hsien, *X. Q. Liu 28700* (PE); Ziyuan, *X. Q. Wang 78003* (NAS). GUIZHOU: Kuei-yang, gorges of Yan-pa, *E. Bodinier 2453* (P); "Kweichow," *M. Cavalerie 3114* (P); Kweiyang, *T. P. Chien 30006* (PE); Thong-kai, *J. Esquirol in 1911* (G); Xingren, *Exped. Guizhou 8466* (NAS); Kao-p'o, *G. Labarde & E. Bodinier 2717* (P); Dejiang Hsien, *N Guizhou Exped. 1747* (NAS); Rongjian, *S Guizhou Exped. 3072* (NAS); Kaili, *S Guizhou Exped. 5542* (NAS); Tsingchen, Wha-chou, *S. W. Teng 90639* (A); Guangcheng, Ma-an-shan, *Y. Tsiang 8597* (NAS, NY, PE, S, UC, W); Fanchin Shan, *P. C. Tsoong 3602* (PE). HEBEI: Beijing ("Peking"), *Dr. Bushell s.n.* (NY); "Hopeh," *C. K. Yang 1627* (NAS). HENAN: Lushi Hsien, *K. C. Liou 4873* (PE). HUBEI: Shinshan Hsien, *S. S. Chin 8169* (NAS); Hsing Shan, *Y. Chen 15072* (UC); Yichang ("I-ch'ang"), *W. Y. Chun & S. S. Chien 8169* (UC); Lichuan Hsien, *L. Y. Dai 665* (PE); Nan-t'o, *A. Henry 4640* (K, TI); "Hupeh," *A. Henry 5102* (E, G), *6573B* (US); Laifeng Hsien, *H. G. Li 7146* (PE); Xianfeng Hsien, *H. G. Li 9346* (PE); Shennongjia, *Shennongjia Exped. 315016* (PE); Chengyang Hsien, *T. P. Wang 11540* (PE); Ziqui Hsien, *T. P. Wang 11874* (PE); "W Hupeh," *without collector 665* (WH); "Hupeh," *without collector 267* (WH). HUNAN: Dafobin, *E. Dahlström 253* (S); Ma-ling-tung, Hsin-ming Hsien, *C. S. Fan & Y. Y. Li 531* (BM, G, GH, L, NAS, P, W); Yongshun Hsien, *Hunan Exped. 412* (PE); Nanyue, *K. C. Kuan 188* (PE); Qianyang Hsien, *Z. T. Li 24, 1434, 2840* (PE); Baojing Xing Hsien, *L. H. Liu 9711* (PE). JIANGXI: Huang-yan-Ssu, Lu Shan, *H. C. Cheo 290* (CAS, E, K, NAS, TAI); Shangyou Hsien, *T. L. Chin 263, 805* (PE); Lu Shan, *R. C. Ching 10224* (PE), *Y. Chow 1172* (NAS); Tchong Yun, *P. Courtais in 1922* (NAS); Oyyuen, *P. Courtais 31448* (NAS); Lu Shan, *K. C. Kuan 74355, 74472* (PE); Kien-nan, Tung-lei, Sai-hang-cheung, *S. K. Lau 4178* (BM, G, GH, S, US); Lung-nan Hsien, near Lam-uk, Oo-chi-shan, *S. K. Lau 4722* (BM, G, S, US); Lushan, *H. Migo in 1941* (NAS); Chin-chiang, *O. v. Moellendorf in 1873* (BM); Chiu-ling-shan, Lushan, *A. K. Schindler 350a* (BM); Yungshiu, Ai-ch'eng, Sa-tiu-hong, *Y. Tsiang 10636* (NAS, NY); Lu Shan, *P. C. Tsoong 566, 10033* (PE), *M. J. Wang 923* (NAS); Lichuan Hsien, *M. J. Wang 2295* (NAS, PE); Nanchang Shi, *X. X. Yang 10043* (PE); Wang-cheng Kang, *Y. H. Yang s.n.* (PE); Jinggang Shan, *J. S. Yue 475* (NAS); Wue Hsien, *J. S. Yue 2024* (NAS); Guenagchang, *J. S. Yue 2552* (NAS); Anfu, *J. S. Yue 2957* (NAS); Suichuan, *J. S. Yue 4031* (NAS). JIANGSU: Shanghai, *E. Faber 110/87* (K); I-hsing-wu-fu, *K. Ling 12385* (UC); Yun-tai Shan, Chiu-lung chiao, *F. H. Liu s.n.* (PE); Liyang, *F. S. Liu et al. 2641* (NAS); Yuntai Shan, *F. X. Liu 10727, 10918* (NAS, PE); Yixing, *W. Z. Fang 226, 7964* (NAS). JILIN: Emu Hsien, *H. W. Kung 2000* (PE); Dunhua Hsien, *T. N. Liou 3514* (NAS); Tongmeling, *Y. Yabe in 1918* (NAS). GUANGDONG: no further data, *S. W. Teng 90639* (NAS). LIAONING: Fusong Hsien, *Y. L. Chang & P. Y. Fu 750* (NAS); Fenghuang, *Y. Yabe in 1909* (NAS); Wulong, *Y. Yabe in 1909* (NAS); Caohekou, *Y. Yabe in 1910* (NAS); Qian Shan, *Y. Yabe in 1918* (NAS). SHAANXI: Yang Hsien, *K. T. Fr 5208* (PE); Liuba Hsien, *K. T. Fr 6209* (PE); Yang Hsien, Hua-yang, *S. C. Fu in 1958* (PE); Shang Hsien, *T. P. Wang 16030* (PE). SHANDONG: Lao Shan, Tailingkio, *C. Y. Chiao 2906* (DS, E, GH, K, MT, NAS, NY, PE, S, TAI, UC); Meng Shan, *Exped. Wil. Pl. Shandong 6084* (NAS); Tsinghai, *Zimmermann 428* (G, GH, P). SICHUAN: Feng Hsien, *T. R. Chang 25920* (NAS, PE); Emei Shan, *S. Y. Chen et al. 4265* (NAS); Miy, *S. Y. Chen et al. 10788* (NAS); Emei Shan, *C. Y. Chiao & C. S. Fan 343* (A), *C. L. Chow 6891* (PE), *H. C. Chow 8280* (A); Feng Hsien, *H. F.*

Chow 26849 (PE); Fangure, *H. F. Chow 26894* (NAS); Wushan, *H. F. Chow 109996* (NAS); Nanxi Hsien, *T. L. Dai 10140* (PE); Chenkou Hsien, *T. L. Dai 103177* (PE); Chien-feng-shan ("Tchen-fong-chan"), *P. Delavay 5054* (DS, G, MO, P, US), *5179* (P), *F. Ducloux 2155* (P); Liangshan, *Exped. Pl. Med. Sichuan 28168* (NAS); Emei Shan, *W. P. Fang 32554* (PE); Wu-shan, *A. Henry 7215* (K, NY); Emei Shan, *C. H. Hsiung et al. 32172* (NAS, PE); Nanchuan, *K. F. Lee 63460* (NAS); Nanchuan Hsien, *K. F. Li 63569* (PE), *64859* (NAS, PE); Emei Shan, *T. N. Liou 853* (PE), *T. C. Peng 187* (A); Kiating, *L. Y. Tai 1382* (A); Yaan Hsien, *T. P. Wang 8583* (PE); Guan Hsien, *C. L. Wu 33760* (PE); Nanchuan Hsien, *J. H. Xiong 92879* (PE); Eshan Hsien, *K. H. Yang 56963* (PE); Wuxi Hsien, *K. H. Yang 65142* (NAS, PE); Emei Shan, Fu-hu-shih, *K. H. Yang in 1957* (PE); Emei Shan, *K. N. Yin 191* (A). YUNNAN: Yunnan-sen, *J. Cavalerie 212* (E); Fuming, *P. Y. Chiou 596397* (KUN); Ta-li-fu, E slope of the Tsau-shan range, *G. Forrest 1054* (E, K); Ming-kuang-ho valley, *G. Forrest 8286* (E); Chiu-kuei-ting? (Geugyueh), *G. Forrest 8736* (E); Yunnanfu-Dali Road, Gwangdung, *H. Handel-Mazzetti 4893* (W); Kua-yin Hsien, Man-mai, S of Red R., *A. Henry 9733* (E, K, LE, MO, US); Mei-tzu, *A. Henry 9733A* (K), *9733B* (E, K, MO, NY); Takwan, *NE Yunnan Exped. 555* (KUN); Luchun, *D. D. Tao 981* (PE); Pingbian Hsien, *H. T. Tsai 61191* (A, NAS, PE), *61253* (A, PE), *61352* (NAS, PE), *61483* (A, NAS, PE), *61737* (A, NAS, PE); Ta-p'ing-ch'ang, Chengkang, Snow Range, *T. T. Yü 17237* (A, E); Mien-ning, Taugeh, *T. T. Yü 18092* (A, E). ZHEJIANG: Lishui Hsien, *S. Y. Chang 6693* (PE); Lungquan Hsien, *S. Y. Chang 8768* (PE); Tiantai, *Exped. Nat. Pl. Zhejiang 1380* (NAS); Hsi-tienmu-shan, *Exped. Pl. Res. Zhejiang 29048* (NAS); Ning-po-shan, *E. Faber in 1888* (LE, P, S); Changhua, *Y. Y. Ho 26334* (NAS); Tianmu Shan, *W. Y. Hsia 239* (PE); Tiantai Shan, *Y. L. Keng 997* (PE, UC); Hangzhou, *K. Kimura s.n.* (KYO); Tianmu Shan, *T. N. Liou 6958* (PE); Lisui Hsien, *Lishui Forest School 6103* (PE); Hsi-tienmu-shan, *H. Migo in 1935* (NAS, TI); Longquan, *R. H. Shan 5757* (NAS); Mogan Shan, *C. P. Tsien 61155* (PE); Longquan, *D. S. Tso 22091* (NAS); Lung-ch'ien, *C. Z. Yu in 1958* (NAS).

INDIA. ASSAM: Manipur, Karong, *T. R. Chand 3792* (DS, MICH); Naga Hills, Jotsoma, *N. Bor 6239* (K); Naga Hills, Kegwina, *C. B. Clarke 41176D* (BM, K); Manipur, Ukhrul, *F. Kingdon-Ward 17971* (BM, NY); Naga Hills, Takubama, *W. N. Koelz 25807* (MICH).

JAPAN. HOKKAIDO: around Hakodate, *Albrecht in 1861* (LE); Ishikari, Sapporo, *S. Arimoto in 1893* (GH); Hakodate, the Lakes, *J. Bisset 2839* (BM), *3170* (E); Ishikari, Sapporo, Mt. Maru-yama, *D. E. Boufford & E. W. Wood 19632* (MO); Iburi, Tomakomai Experimental Forest of Hokkaido Univ., *D. E. Boufford & E. W. Wood 19657* (BM, CAS, CM, DS, E, G, GH, K, KYO, LD, LE, MHA, MICH, MO, NCU, NY, P); Hidaka, Shizunai-cho, 14 km ENE of Shizunai, *D. E. Boufford & E. W. Wood 19673* (KYO, MHA, MO); Kushiro, NW edge of Lake Toro-ko, *D. E. Boufford & E. W. Wood 19744* (CM, G, K, KYO, MHA, MO, NCU, PE); Ishikari, Sapporo, Mt. Teine-yama, *D. E. Boufford & E. W. Wood 19858* (CM, MHA, MO); Horobetsu, *U. Faurie 2630* (DS, G, KYO, P); around Junsainuma, *U. Faurie 6307* (KYO, W); in the forests of Nayoro, *U. Faurie 6308* (BM, KYO, W); near Mororan, *U. Faurie 6309* (BM, KYO); Mori, *U. Faurie 6310* (BM); Ishikari, Sorachi-gun, Manju, *F. C. Greatrex in 1915* (SAP); Hakodate, *F. C. Greatrex 266* (SAP); Tokachi, Tokachi-gun, Urahoro, *K. Hori in 1896* (SAP); Oshima, Kumai-shi, *D. Hoshi in 1944* (SAP); Ishikari, Barato, *K. Ito in 1962* (SAP); Kazusa, *Z. Iwamoto in 1883* (SAP); Iburi, Shizukari, *T. Kawakami in 1892* (SAP); Oshima, Mt. Fuku-yama, *T. Kawakami in 1892* (SAP); Iburi, Muroran, *S. Kitamura in 1935* (KYO); Hakodate, *C. Maximowicz in 1861* (GH, K, L, NY); Ishikari, Sapporo, *K. Miyabe in 1882* (NY); Ishikari, Barato, *K. Miyabe in 1884* (SAP); Oshima, Fukuyama, *K. Miyabe & Y. Tokubuchi in 1890* (TI); Oshima, Ishizaki, *K. Miyabe in 1890* (SAP); Iburi, Rebunge-toge, *K. Miyabe in 1890* (SAP); Ishikari, Otoibokke, Sorachi, *K. Miyabe in 1891* (SAP); Iburi, Usu, *K. Miyabe & K. Hino in 1931* (SAP); Oshima, Fukushima, *K. Munakata in 1960* (MASS, MHA, MO); Abashiri, Memambetsu, *T. Nakano in 1955* (SAP); Kawakami-gun, *S. Okamoto in 1943* (KYO); Kitami, Ufutsu, *S. Okamoto in 1952* (KYO); Tokachi, Kami-ashi-yori, *S. Okamoto in 1955* (KYO); Tokachi, Shibetsu, Mt. Yoshit-sune, *S. Okamoto in 1959* (KYO); Kushiro, Lake Kusharo, *S. Okamoto 1072* (KYO); Hidaka, Saru-gun, Tomikawa, *Y. Takahashi in 1963* (SAP); Shiribeshi, Zenibako, *Tekee et al. in 1931* (SAP); Kushiro, Lake Kutcharo, *M. Tatewaki in 1933* (SAP); Oshima, Fuku-yama, *Y. Tokubuchi in 1888* (SAP); Hakodate, *Y. Tokubuchi in 1888* (SAP, TI); Hidaka, Horoizumi, *Y. Tokubuchi in 1892* (MO, SAP); Chitose-gun, Aosari-toge, *Y. Tokubuchi in 1893* (GH, SAP); Oshima, Kishu, *Y. Tsukamoto in 1940* (KYO); Kushiro, Toro, *A. Umezawa in 1956* (SAP); Shiribeshi, Yoichi, *I. Yamamoto 4269* (KYO); Shiribeshi, Oichi, *I. Yamamoto 4978* (KYO); Tokachi, Ikeda, *H. Yokoyama in 1936* (TI), *H. Yokoyama & H. Hara 3248* (SAP); Tokachi, Ikeda-cho, Suigen-shi, *H. Yokoyama 4252* (SAP). HONSHU: AICHI PREFECTURE: Miwa-mura, *G. Murata 6597* (KYO); Horaiji Mts., *M. Takeuchi in 1945* (TI). AKITA PREFECTURE: Tohi-shima Island, Akumi-gun, *G. Koidzumi in 1927* (KYO); Oga Peninsula, Monzen, *R. Mochizuki 0819* (KANA); Mt. Moriyoshi-yama, Naka-mura to the summit, *H. Ohashi 4855* (TI); Nibetsu, near Seismic Observatory of Tohoku Univ., *K. Sohma 1575* (MAK); Akita city, Tegata, *S. Tanaka in 1960* (KANA); Yamamoto-gun, Hi-yama, *without collector in 1925* (MAK 117754). AOMORI PREFECTURE: Aomori city, *U. Faurie 7* (KYO); vicinity of Aomori, *U. Faurie* 955

(P); Aomori, *U. Faurie 5095* (BM, G, KYO); Higashitsurugu-gun, Miyumaya-cho, Mt. Yakataishi-dake, *N. Fukuoka 6851* (KYO); Imabetsu, Okawahira, *K. Hosoi in 1949* (KANA); Minamitsugaru-gun, Owani, Mt. Nijima, *K. Hosoi in 1950* (KANA); Tsugaru Peninsula, Higashitsugaru-gun, from Sanyoshi to Katsura-zawa along Sanyoshi R., *H. Koyama 1584* (KYO, TNS); Shimokita Peninsula, Shikkari, Kukito-no-misaki, *H. Ohashi 4554* (TUS); Minamitsugaru-gun, Miyama-mura, Misukawa, *S. Okamoto in 1963* (KYO); Yuno-shima, *Y. Takeuchi in 1960* (TUS); Shimokita Peninsula, Bushi-domari, *K. Yoshioka & T. Kanebo in 1964* (TUS); Shimokita Peninsula, Sarugamori, *K. Yoshioka & K. Sugawara in 1964* (TUS). CHIBA PREFECTURE: Ichikawa, *K. Hisauchi 1637* (L, TI); Umbo, Mt. Kiosumi, *K. Miura in 1910* (SAP). FUKUI PREFECTURE: Obana city, *T. Izaki in 1910* (MAK); Fukui city, Mt. Asua, *H. Kimura et al. in 1965* (KANA); Eiheiji, *S. Kitamura in 1961* (KYO); Tsuruga city, *S. Kitamura & G. Murata 2088* (KYO); Yoshida-gun, Eihaiji-Urayama, Mt. Daibutsuji-yama, *H. Koyama 1086* (KYO, MAK, SHIN, TNS); Nyu-gun, Iao-mura, Ogawa, *M. Maeda 535* (KANA); Nyu-gun, Mt. Oshi-san, *G. Masamune 5232* (KANA, MAK); Imatachi-gun, Imatachi-cho, Nakatsu-yama, *S. Mizukami in 1966* (KANA); Tsuruga city, Ikegawachi, *S. Tanaka in 1964* (KANA); Nanjo-gun, Kawano-mura, Imaizumi, *S. Watanabe 28301* (KANA); Ichijo-taki, *T. Yamamura in 1937* (KANA). FUKUSHIMA PREFECTURE: Sukagawa-mura, *R. Endo in 1912* (TUS); Yama-gun, Bandai-mura, Mt. Umatake-san, *M. Furuse in 1957* (A, NA, S). GIFU PREFECTURE: Mugi-gun, Itadori-mura, from Shimaguchi to Shiraki Pass, *N. Fukuoka & K. Yamashita 35* (KYO), *48* (KANA); Mugi-gun, Itadori-mura, vicinity of Kadode, *N. Fukuoka & K. Yamashita 231* (KANA, KYO); Mt. Yoro, *T. Ito in 1890* (TNS); Mt. Jikkyoku-toge in Nakasendo, *T. Ito in 1891* (TNS); Oono-gun, Asahi-mura, Kurumijima, *G. Murata et al. 418* (KYO); Gunjo-gun, Yawata-cho, *without collector in 1904* (MAK 117773). GUNMA PREFECTURE: Usui-gun, Hakun-zan in Mt. Myogi-san, *G. Murata 27485* (KYO); Usui-gun, Gokan-mura, Mt. Chogenji, *Nakajima in 1933* (KYO); Hanashiki-onsen, *J. Ohwi in 1929* (KYO). HYOGO PREFECTURE: Kinosaki-gun, Mikata-mura, Mt. Sofuka-dake, *Y. Araki in 1932* (KYO); Yabu-gun, Sekinomiya-cho, NE foot of Mt. Hyonosen, *D. E. Boufford & E. W. Wood 19553* (BM, CAS, CM, E, G, GH, K, KYO, MHA, MO, NCU, NY, P, PE, S, SHIN, UC); Yabu-gun, Oya-cho, Ikada, *D. E. Boufford et al. 19577* (K, KYO, MO); Mikata-gun, Onsen-cho, Kiri-taki waterfall, *D. E. Boufford et al. 19593* (BM, CM, GH, KYO, LE, MHA, MO, NY, P, UC), *G. Murata 20679* (KYO); Shiso-gun, Haga-cho, Tokura, *D. E. Boufford et al. 19585* (CM, KYO, MHA, MO); Nunobiki, *T. Fujimoto 6* (KANA); Mikata-gun, Mt. Suga-no-sen, *N. Fukuoka & Y. Inamasu 722* (KANA, KYO); Kanzaki-gun, Ichikawa-cho, *I. Hashimoto in 1902* (MAK); Shikama-gun, Mt. Seppiko, *M. Hiroe 6271* (KYO); Kanzaki-gun, Okawachi-cho, Kawakami, *M. Hiroe 17395* (KYO, UC); Hikami-gun, Hikami-mura, Iso, *S. Hosomi in 1935* (KYO); Mikata-gun, Mikata-mura, Koshido-dani, *S. Hosomi 9902* (KYO); Mt. Roko, *S. Kuriyama in 1928* (MAK); Miki-shi, Hosokawa-cho, *G. Murata & H. Nishimura 297* (KYO); Hikami-gun, Hikami-cho, Kora, *G. Murata 19954, 19965* (KYO); Shiso-gun, Haga-cho, Tokura, *G. Murata 20355* (KYO); Sayo-gun, Nanko-cho, Mt. Hunakoshi-yama, *G. Murata 33779* (KYO, MO); Shiso-gun, Haga-cho, Onzui, *M. Tagawa & K. Iwatsuki 5206* (KYO); Shiso-gun, Chikusa-mura, Nabegatani Government Forest, *M. Tagawa 6367* (KYO). IBARAGI PREFECTURE: Kamiura city, Kidayo-mura, *without collector in 1901* (MAK 117792); Tsuchiura city, *without collector in 1905* (MAK 117757). ISHIKAWA PREFECTURE: Kanazawa city, Okushinbo, *S. Enu in 1967* (KANA); Kanazawa city, Okua-cho, *E. Etchu in 1967* (KANA); Mt. Ioo, Nishio-daira, Kunimi Pass, *N. Fukuoka 4327* (KANA); Suzu-gun, Ogi, *Furuike in 1958* (KANA); Suzu-gun, Doronoki, *Furuike in 1958* (KANA); Mt. Udatsu, *R. Hara in 1957* (KANA); Mt. Hakusan, *T. Ichimura 1441* (KANA); Kanazawa city, Noda-cho, *R. Ikeda in 1953* (KANA); Komatsu city, Osugidani, *K. Kaburagi in 1963* (KANA); Kashima-gun, Kashima-cho, *R. Kaga in 1965* (KANA); Hoshi-gun, Munzen-cho, Minazuki, *T. Kikuchi 676* (KANA); Kanazawa city, Mt. Utatsu-yama, *G. Masamune in 1957* (KANA, KYO); near Kanazawa, Kurokabe, *G. Masamune 5176* (KANA); Kasime-gun, Sekido-san, *G. Masamune 5627* (KANA); Hugeshi-gun, between Urakami & Minazuki, *G. Masamune 5823* (KANA); Hugeshi-gun, between Tsurugiri & Takatsume-yama, *G. Masamune 12473* (KANA); Hodai-gun, Mt. Isurugi, *G. Masamune 5627* (KANA); Mt. Kyoga-take, Oono city, *G. Murata & T. Shimizu 398* (KYO); Ishikawa-gun, *H. Nakagawa 0588* (KANA); Hoshi-gun, Yanagida-mura, *S. Noriichi in 1969* (KANA); Hoshi-gun, Mitsui, Bantan-san, *N. Satomi in 1963* (KAG); Ishikawa-gun, Mt. Gasseki, *T. Shimozawa in 1953* (KANA); Kanazawa city, Kanazawa Castle, *S. Tanaka in 1960* (KANA); Kanazawa city, Mt. Urotatsu, *S. Tanaka in 1962* (KYO); Mt. Udatsu, *S. Tanaka in 1962* (KANA); Ishikawa-gun, Tsurugi-cho, *I. Umeda in 1954* (KANA); Mt. Hodatsu, *S. Yamamori 3805* (KANA); Botanical Garden, Univ. of Kanezawa, *S. Yoshitake & S. Kaneda in 1966* (TI). IWATE PREFECTURE: Morioka city, Asagishi, *M. Kikuchi in 1967* (TNS); Tensho-shi, *T. Naruse in 1965* (KANA); Hosoura, *S. Suzuki in 1952* (UC, WTU); Takada city, Otomo, *G. Toriba in 1901* (MAK). KANAGAWA PREFECTURE: Jinmuji, *Y. Asai in 1952* (TI); Yokohama, *J. Bisset 629* (E, K), *630* (BM), *F. Dickins 2031* (PH), *C. Maximowicz in 1862* (LE); Enoshima, *S. Momose 286* (TI); Hakone, Ashino-ko, *S. Okamoto in 1966* (SHIN); Hakone, *P. Savatier 412* (P); Hakone, Sengoku-bara, *S. Suzuki in 1951* (UC, WTU). KYOTO PREFECTURE: Kumano-gun, Kawakami-mura, Mt. Kyoruji-yama, *Y. Araki 9643* (KYO); Kasa-gun, Kamogami-mura, Mt. Oe-yama, *Y. Araki 9647* (KYO, TNS); Kyoto city, Sakyo-ku, *D. E. Boufford 19604* (MO);

Kyoto city, WNW side of Mt. Daimonji-yama, *D. E. Boufford & S. Mitsuta 19959* (CM, KYO, MO); Takeno-gun, Yasaka-cho, Noma, Sukawa, *N. Fujita & I. Kojima 99* (KYO); N of Kyoto, Kyu-hanase-kaido, *M. Hiroe 15041* (UC); Kitakuwada-gun, Miyama-cho, Choji-dani in Ashiu Experimental Forest of Kyoto Univ., *K. Iwatsuki 5521* (KYO); Mt. Oe-yama, *N. Kinoshita in 1906* (MAK); between Takai & Kiyotaki, *S. Kitamura in 1936* (KYO); Mt. Kibune, *S. Matsuda in 1892* (KYO); Daihi-zan, N of Kyoto, *G. Murata 9895* (KYO); Ashiu Experimental Forest of Kyoto Univ., *S. Okamoto in 1936* (KYO), *S. Okamoto in 1951* (SHIN); Wachi, *M. Ota in 1966* (KANA); Kyoto city, Mt. Hiei, *M. tagawa 284* (KYO); Hanase-toge, N of Kyoto, *M. Tagawa 4008* (KYO, TNS). MIE PREFECTURE: Kameyama city, from Sakamoto to the summit of Mt. Nonobori, *N. Fukuoka 5105* (KYO); Inabe-gun, Ishigure-mura, Mt. Ryuga-dake, *N. Fukuoka 5978* (KYO); Ichishi-gun, Misugi-mura, near Mt. Miune, *N. Fukuoka 6083* (KANA, KYO); Isshi-gun, Taro-mura, Mt. Kuro-san, *H. Kanai in 1962* (TI); Ise city, Mt. Asama, *H. Kanai 6816* (H, TI); Experimental Forest of Mie Univ., *S. Kitamura in 1963* (KYO); Watarai-gun, Shimadzu-mura, *Kowana 75* (MAK); Ichishi-gun, Misugi-mura, Hiraku-ra, *G. Murata 18393, 18409* (KYO); Yuno-yama-onsen, *G. Nakai 4617* (KYO); Naga-gun, Kozu-mura, *G. Nakai 4764* (KYO); Kamiji-yama, Ise Shrine, *A. Nitta 11357* (KYO); Azan-gun, Ueno-cho, *Sadaishi 6932* (MAK); Ise Shrine, *Y. Sakamoto in 1938* (KANA). MIYAGI PREFECTURE: Miyagi, *F. & C. Baker in 1914* (CAS); Kinkazan Island, Ojika-gun, *M. Kikuchi in 1967* (TNS); Natori-gun, Akiu-cho, SE foot of Mt. Ohazuma, *H. Koyama 4129* (KYO); Miyato-jima, *T. Kyogoku in 1956* (TUS); Ishimaki-cho, *Odashima in 1906* (MAK); Sendai, Aobayama, *K. Sohma 1574* (MAK, MO, TUS); Mt. Kurikoma, *S. Sugaya et al. in 1952* (TUS); Matsushima-cho, Mt. Tomi-yama, *E. W. Wood & D. E. Boufford 3966* (KYO, MO). NAGANO PREFECTURE: Chiisata-gun, Shioda-cho, Bessho-onsen, *N. Kitagawa 5385* (KYO); Shimonakai-gun, vicinity of Jigoku-dani, *M. Minemura 837* (MAK); Uka-wairi, Susawatari to Higashi-sawaguchi, *S. Momose in 1934* (TI); Kamiminochi-gun, *M. Murasawa in 1906* (MAK); Iiyama city, *T. Saito in 1906* (MAK); Koshoku-shi, Oike Pond, S of Obasute, *T. Shimizu 17035* (SHIN); Hanishina-gun, Mt. Kyodai, *T. Shimizu 17374* (SHIN); Mt. Togakushi, *H. Tamura in 1923* (KAG); Kitasaku-gun, Bogetsu-cho, *without collector in 1925* (MAK 117768). NARA PREFECTURE: Mt. Katsuragi, *H. Ohashi et al. 632* (KYO, TI); Mt. Muro, *M. Tagawa 3494* (KYO). NIIGATA PREFECTURE: vicinity of Kashiwazaki city, *K. Abe in 1905* (MAK); Mt. Myojyo, *T. Ajima 4316* (KANA); Sado Island, *U. Faurie 1337* (KYO); Nakakambara-gun, Kanezu-mura, *S. Ito in 1904* (SAP); Kitaonuma-gun, Yunotani-mura, between Oyu & Kamanoyu, *S. Kitamura & G. Murata 2705, 2723* (KYO); Awa-shima Island, *K. Mori in 1956* (KANA); Sado Island, Mt. Todara-mine, *G. Murata 6457* (KYO); Nishi-kubiki-gun, Mt. Myojo, *T. Shimizu 12952* (S, SHIN); Kirita, Arakawa-machi, *S. Togasi 1797* (A, BM, COLO, DAO, E, G, H, K, KAG, KANA, KYO, MO, MTJB, NA, NTUF, NY, P, S, SAP, TI, TNS, TUS, UPS, US, WTU); Shiro-yama, E foot, *without collector & date* (MAK 117790). OKAYAMA PREFECTURE: Shin-zan, *S. Arimoto in 1903* (SAP). OSAKA PREFECTURE: Mino city, *S. Matsuda in 1896* (KYO); Mino city, from Masano-choya to Katsuo-ji, *A. Nitta 10794* (KYO); Kitakawachi-gun, Shijonawate-jinja, *K. Seto 6974* (OSA). SAITAMA PREFECTURE: Noda city, *F. Atsusawa in 1910* (MAK); Minamisaitama-gun, Sakurai-mura, *R. Ito 717* (MAK); ca. 2 km S of Urawa, *T. Koyama 309* (DAO); Segasaki in Urawa, *T. Koyama 5221* (DAO). SHIGA PREFECTURE: Higashiasai-gun, Asai-machi, vicinity of Takayama, S foot of Mt. Kanakuso, *N. Fukuoka 5204* (KYO); Inukami-gun, Taga-cho, Hozuki, Mt. Nabejiri-yama, *H. Koyama 5477* (KYO, MO), *5481* (KYO); Katata-cho, Umenoki to Kowai, *G. Murata 17352* (KYO); Mt. Ibuki-yama, Ueno to the top, *T. Shimizu 0654* (KYO). SHIMANE PREFECTURE: Kanoashi-gun, Kakino-cho, Suzuno-otani-yama, *I. Miyamoto 2861* (MAK); Hirata city, Saka-cho, *I. Miyamoto 62084* (MAK); Hirata-cho, Gakuenji, *G. Murata 11646* (KYO); Oki Island, Oki-gun, *without collector in 1889* (MAK 117779). SHIZUOKA PREFECTURE: Miyake-jima Island, *N. Hayashi 239* (KYO); Fuji-gun, Shiraito-mura, Inokashira, *H. Kanai in 1962* (TI); Minamiizu-cho, Nanigatsu, *H. Naguchi 4645* (KAG); Izu, Amagi-toge, *M. Tohyama in 1953* (SAP). TOCHIGI PREFECTURE: Nikko-kaido, Ninami, *K. Miyabe in 1882* (SAP). TOKYO PREFECTURE: Hachijo Island, Mt. Hachijo-fuji, *M. Hori in 1964* (OSA); Setagaya-ku, Todoroki, *S. Kobayashi 751* (CAS); Nakano-ku, Arai, *T. Makino in 1896* (MAK); Dokanyama, *T. Makino in 1900* (MAK, S); Shinbasu-no-ike Pond, *S. Matsuda in 1890* (KYO); Tokyo, *J. Matsumura in 1878* (US); Musashi, Koshigaya, *J. Ohwi 333* (A, B, BM, DAO, E, G, H, KAG, KANA, KYO, L, MICH, MO, MT, MTJB, NA, NTUF, NY, S, TI, TNS, TUS, UC, UPS, US, W); Komae, *S. Suzuki in 1949* (K, UC); Nippara, *S. Suzuki 364* (A); Nakano near Tokyo, *H. Takeda 253* (K); Tokyo, *T. Terasaki in 1908* (K); Nakano near Tokyo, *T. Uno 253* (BM); Narima-ku, Shijakui, *without collector in 1939* (MAK 117761); Miyake-mura, Miyake Island, *without collector in 1937* (MAK 117771). TOTTORI PREFECTURE: Tottori city, Matsugami, *A. Tanaka 20724* (KYO). TOYAMA PREFECTURE: Fuko-cho, Yamamoto, *H. Furuike in 1955* (KANA); Mt. Tateyama, *T. Ichimura in 1890* (KANA); Iguchi-mura, Maruyama, *Ishioka in 1973* (KANA); Shimoshinkawa-gun, Ogawa-onsen, *H. Kanebo in 1962* (KANA); Nakanikawa-gun, Kamiichi-mura, Mt. Daikamine, *N. Kurosaki 2123* (SHIN); Nakanigawa-gun, Kamiichi-mura, Nagara Pond, *N. Kurosaki 2191* (KYO); Nakashinkawa-gun, Uechi-cho, Oiwa, *N. Kurosaki 2262* (KANA); Kurobe city, *M. Uishiro in 1905* (MAK); Io-zen, *K. Yoda 278* (KANA). WAKAYAMA PREFECTURE: Higashimuro-gun, Shinokawa-dani, *T. Kodama in 1951* (OSA); Minamimuro-gun,

Kuki-mura, *G. Murata 9973* (KYO); Awo-ga-shima, *T. Tuyama in 1933* (TI); Nishimura-gun, Daito-mura, Tsuruji-jinja, *T. Yamamoto 374* (KYO); Mt. Koya-san, *without collector in 1902* (MAK 117777). YAMAGATA PREFECTURE: Higashine city, Makino, *D. E. Boufford & E. W. Wood 19877* (CM, KYO, MHA, MO, PE); near Koshigoe, *F. Greatrex in 1935* (K); Kitamura-yama-gun, Komatsu-sawa, *S. Inoue in 1914* (MAK); Tsuruoka city, Mt. Kimpo-yama, *K. Mori in 1897* (MAK); Tobi-shima Island, *K. Mori 17043* (S); between Yamadera & Futakuchi Pass, *H. Ohashi in 1960* (TUS); from Fukuura to Mt. Chokai, *H. Ohashi 8682* (TI); Akumi-gun, Fukura-mura, Mega, *H. Ohashi 10610* (TI); Sakata city, *I. Sato in 1912* (MAK); near Atsumi village, *E. Walker 7347* (US). YAMAGUCHI PREFECTURE: W of Hiroshima city, base of Mt. Shiro-yama, Senjo-kubara, *L. Charette 1381* (COLO, MO, UC, US, VT), *1862* (MO, NA, S, UC, US, VT); Kuga-gun, Hirose-deai, *H. Migo in 1952* (KANA); Tsuno-gun, Shikano, *H. Migo in 1953* (KANA); Kuga-gun, Takamori, *H. Migo in 1954* (KANA); Iwai-shima Island, *H. Migo in 1956* (KANA); Kuga-gun, Mikawa, Miyano-kushi, *H. Mitsue in 1952* (KYO); Kinkei-no-taki, *T. Nakai & M. Maruyama in 1949* (TNS); Namera-yama, Higure-zawa, *T. Nakai & N. Maruyama in 1949* (TNS); Abu-gun, Tokusa-mura, *H. Ohaba s.n.* (KYO); Tokuyama city, Nagaho, Ryumonji, *K. Oka 32113* (KYO); Iwakuni city, Shiro-yama, *M. Tagawa 2494* (KYO); Chofu-mura, *without collector, 26 July* (KAG). YAMANASHI PREFECTURE: Nishiyatsushiro-gun, *H. Kanai in 1957* (TI); Lake Yamanaka, *T. Makino in 1936* (MAK); Kaminohara-cho, Gunnai, *S. Okamoto in 1935* (KYO); Kita-tsuru-gun, Kamina-hara-mura, Tanagashira, *S. Okamoto in 1935* (KYO); Otsuki city, Mt. Ogi-yama, *S. Okamoto in 1935* (KYO). KYUSHU: FUKUOKA PREFECTURE: Kasuya-gun, Sasakuri-mura, Mt. Wakasugi, *K. Ishikawa 200158* (LD, NA, NTUF); Kaho-gun, Kaho-machi, Mt. Kosho-san, *S. Imae 8462* (KANA); Asakura-gun, Hoshujama-mura, *K. Nagayoshi in 1961* (KAG); Tagawa-gun, Kawara-machi, Mt. Kawara-dake, *T. Shimizu 0276* (KYO). KAGOSHIMA PREFECTURE: near Fukiage, *S. Hatusima 20373* (KAG); between Hanaze & Hetsuke Pass, *S. Hatusima 20429* (KAG); Mt. Shiba, *S. Hatusima 21041* (KAG); Mt. Takakuma, *S. Hatusima 21165* (KAG); Mt. Takakuma Experimental Forest, *Kawagoe 5065* (KAG); from Kushira to Uchi-no-ura, *T. Naito in 1926* (KAG); Mt. Takakuma Experimental Forest, *T. Naito in 1926* (KAG); Koshiki-jima Island, *S. Sako 1488* (KAG); Kagoshima, *without further data* (TI). KUMAMOTO PREFECTURE: Ago-gun, Kukino-mura, *K. Fukunaga 5376* (KAG); Aso, Mt. Kitamuki-yama, *S. Imae 10510* (KANA); Hottaku-gun, Mt. Kimpo-zan, *H. Kamizuma in 1906* (MAK); Kami-mashiki-gun, Chuo-mura, *Nishiyama & Y. Shimada 12681* (KYO); Gokanosho, Momiki, *S. Sako 954* (KAG), *1117* (KAG, KANA); Gokanosho, Kureko, *S. Sako 1304* (KAG); Yatake, Hitoyoshi city, *S. Sako 6576* (KAG); Kuma-gun, Itsugi-mura, from Motoi-dani to Hotokeishi, *T. Shimizu 4757* (KYO); Kuma-gun, Itsugi-mura, W of Itagi, from Toji to Tenguiwa, *T. Shimizu 5078* (KYO); Yatsushiro-gun, Toyo-cho, Akai-yama, *Y. Simada 10199* (KYO); Kumamoto city, Ikedai-mura, *without collector in 1905* (MAK 117787). NAGASAKI PREFECTURE: Fukue city, Goto Islands, *S. Hatusima 16798* (KAG); Tsushima Island, Shinoagata-gun, Mizushima-cho, NW foot of Mt. Matsu-yama, *H. Koyama 2761* (KYO, TNS); Tsushima Island, Shimoagata-gun, N foot of Mt. Tatera, *H. Koyama 3020* (KYO, TNS); Nagasaki, *C. Maximowicz in 1863* (BM, LE, W), *R. Oldham 278* (BM, G, K, L, NY, P, S, W); Tsushima Island, *Y. Yabe 6921* (MAK); Tsushima Island, Iwahara, Aga-toichi-buchi, *Y. Yabe 6925* (MAK); Sasebo city, Hiu-mura, *without collector in 1904* (MAK 117788). SHIKOKU: EHIME PREFECTURE: Uwa-jima, Toko-name, *G. Koidzumi in 1934* (KYO). KAGAWA PREFECTURE: Kida-gun, Mt. Goken-san, *S. Matsumoto in 1905* (MAK). KOCHI PREFECTURE: Takaoka-gun, Mt. Yokogura, *M. Hori in 1957* (OSA); Nakamura city, Hyakuwarai, *Y. Kanematsu 186* (MAK); Mt. Nishiki-yama, *S. Kitamura in 1949* (KYO, MICH); Suzaki city, Boku-no-kawa, *T. Makino in 1889* (MAK); Iwado, *T. Makino in 1892* (MAK); Nagaoka-gun, Mt. Shiraga-yama, *G. Murata 10876* (KYO); Nagaoka-gun, Otoya-mura, Mt. Kajigamori, *G. Murata 18679, 18682* (KYO); Takaoka-gun, Shimohayama-mura, State Forest of Todoro-yama, *M. Tagawa 2707* (KYO); Mt. Yokogura, *S. Takafugi in 1974* (KYO); Nanokawa, *S. Watanabe in 1892* (GH, K); Kuromori, *without collector in 1888* (TI). TOKUSHIMA PREFECTURE: Oe-gun, Yamakawa-cho, Mt. Takaetsu-yama, *T. Kasai in 1917* (MAK); Anan city, Aratano-cho, Tairyuji, Ryuno-iwaya, *H. Koyama 1134* (KYO, TNS); Miyoshi-gun, Nishi-iyayama-mura, Mt. Kunimi-yama, *G. Murata 7692* (KYO); Kaibu-gun, Mugi-mura, *without collector in 1909* (MAK 6920).

KOREA, NORTH. Vicinity of China-Korea border, *T. Kanashiro 5573* (KYO); Kannan, Tokugen near Onen-san, *S. Kitamura in 1932* (KYO); Fuzan city, *H. Migo in 1969* (KANA).

KOREA, SOUTH. Cheju-do (Quelpaert Island), *I. C. Chung 3098* (TNS), *U. Faurie 1833* (G); Hallai-san, *T. Nakai in 1913* (TI); Mt. Chii, *S. Okamoto 17936, 17937* (KYO); Ham-Puk, Ra-nan, *T. Saito in 1935* (KYO); Cheju-do (Quelpaert Island), Hongno, *E. Taquet 131* (G), *831* (G, K), *4259* (G, LE).

KOREA, LOCALITIES UNKNOWN: Diamond Mts., *Mrs. R. Smith 686* (US); Kangkai, *R. G. Mills 774* (TI).

LAOS. Nong Et, *M. E. Poilane 16823* (P).

VIETNAM. Tonkin, Cha Pa, *M. Petalot 5094* (NY, P, US), *M. Hautefeuille 110* (P); Tonkin, Ta Phing, *E. Poilane 12825* (P); Mt. Pia-duac, Vam Kep, *M. Petalot in 1922* (P).

Circaea mollis most closely resembles *C. lutetiana* subspp. *canadensis*, *quadrisulcata*, and *lutetiana* but can be distinguished from the former two subspecies by the pubescent stems, green buds and sepals, and darkened nodes and from the last by the globose, or nearly globose, strongly sulcate, ribbed fruits. From all subspecies of *C. lutetiana*, *C. mollis* differs by having lanceolate or broadly lanceolate leaves with cuneate leaf bases, in the generally smaller size of all floral parts, and in the shorter pedicels.

Circaea mollis is the most robust species of the genus and is approached in size only by the largest plants of *C. cordata*. It is also the only species in Asia that may be somewhat weedy. Although it is never found in recently disturbed habitats, it is quite frequent in later successional stages, in thickets along streams, roadsides, and abandoned rice paddies. It is the most common species of *Circaea* in *Cryptomeria* plantations throughout Japan at low elevations. *Circaea mollis*, under favorable conditions, may form extensive colonies of many square meters, but rarely dominates an area, tending most often to be intermixed with other coarse herbs, low shrubs, and vines. It is also the only species that approaches subtropical areas, ranging into the southernmost parts of the warm temperate zone at low elevations. Northward, *C. mollis* becomes local and is replaced in some similar situations by *C. lutetiana* subsp. *quadrisulcata*, which, however, does not occur in situations as disturbed as some of those in which *C. mollis* grows.

Except for size differences, which appear to be related to local environment, *Circaea mollis* is remarkably invariable throughout its range and is probably the least variable of the bilocular species of *Circaea*. The few characters that appear to be plastic are the shape of the leaf base, fruit shape, and presence or absence of a minute bracteole at the base of the pedicel. The presence of a bracteole and various shapes of the leaf base do occur sporadically throughout the range of the species, whereas plants with more slender fruits are more common in the western part of the range. Léveillé (1907) based his *C. coreana* var. *sinensis* partially on this feature, which is much more pronounced in immature fruits. Mature fruits of such plants, however, approximate in shape and size fruits from throughout the range. This very slight difference does not warrant formal taxonomic recognition.

Bracteoles are infrequent in *Circaea mollis* and cannot be used as a diagnostic character. When bracteoles do occur, they are most commonly found subtending the lowermost pedicels of a raceme, and they may be lacking from the upper pedicels of the same plants. Occasionally they may be found only beneath a few of the middle pedicels or sporadically under non-adjacent pedicels. Shape of the leaf base may also differ on the same plant. Commonly, the lowest leaves are more apt to have rounded bases while those above may have broadly to narrowly cuneate bases. The lower leaves are usually deciduous by the time of flowering and fruiting and therefore not noticeable. The rounded leaf bases of immature plants make certain identification of these plants difficult since they may resemble the minutely pubescent forms of *C. erubescens* or the hybrids, *C.* × *dubia* (*C.*

cordata × *C. erubescens*) and *C.* × *ovata* (*C. cordata* × *C. mollis*). In flower or in fruit, there is no confusion among any of these.

4. Circaea lutetiana L., Sp. Pl. 9. 1753.

Erect or rarely decumbent at the base, 1.2–9 dm tall, simple or rarely branched below the inflorescence, forming long rhizomes without tuberous thickenings, which give rise to the following year's plants from their tips. Plants glabrous to densely pubescent, the stem with one or a combination of the following hair types: soft, falcately recurved hairs, 0.2–0.3 mm long; capitate and clavate-tipped hairs ca. 0.4 mm long; soft, sharp-pointed, straight or slightly curved, patent hairs, 0.5–1 mm long. The petioles with soft, short, falcate, upwardly curved hairs or with hairs as on the stem. Leaves glabrous or, more commonly, pubescent, especially near the base of the blade and along the main veins on the lower, and occasionally also on the upper surface, with soft falcate hairs ca. 0.2 mm long, occasionally also with long straight hairs ca. 1 mm long if these present on the stem; interveinal areas not at all or less densely pubescent; leaf margins with short, curved cilia and also with long straight hairs if these present on the stem. Axis of the inflorescence densely covered with capitate and clavate-tipped glandular hairs, 0.2–0.4 mm long, the pedicels less densely so. Stem green or rarely the nodes brownish or purple. Leaves horizontally spreading, sometimes drooping at the tips, green, opaque; those below to those just above the middle of the stem the largest, (3–)4.5–16 cm long, 2–6(–12) cm wide, becoming gradually reduced in size upward and eventually bractlike and alternate at the base of the inflorescence; gradually reduced in size downward. Leaf shape highly variable, ranging from very broadly elliptic to deltoid ovate but most commonly ovate, lanceolate ovate or oblong ovate; short to long acuminate to the obtuse or subacute apex, very broadly cuneate to subcordate but most commonly rounded or truncate at the base, denticulate. Petioles (0.6–)1.3–5.5(–7.5) cm long, sparsely to densely pubescent with soft, upwardly curved falcate hairs ca. 0.2 mm long or, in subsp. *lutetiana*, sometimes with longer, straight or slightly curved hairs, 0.5–0.8 mm long, intermixed if these present on the stem; commonly with reduced branches arising in the axils. Inflorescence densely pubescent with capitate and clavate-tipped glandular hairs, 0.2–0.4 mm long; terminal on the main stem and rarely at the tips of short, uppermost axillary branches; a simple raceme or the raceme branched near the base, the lateral branches subtended by reduced leaves or leaflike bracts; the terminal raceme, from the uppermost reduced leaf or leaflike bract, 1.5–3 cm long at initiation of flowering, to 30(–40) cm long at cessation of flowering; the lateral racemes, 2–6 cm long at initiation of flowering, to ca. 20 cm long at cessation of flowering, subequal in length on the same plant. Flowering pedicels, 1.9–5.2(–9) mm long, perpendicular to the axis of the raceme, pubescent, with capitate and clavate-tipped glandular hairs, 0.2–0.3 mm long, with or without a minute setaceous bracteole, 0.2–0.4(–7) mm long, at the base. Fruiting pedicels 3–6.5(–10) mm long. Buds pubescent, with short, soft, glandular hairs ca. 0.1 mm long, rarely glabrescent; green or purple, especially towards the apex, elliptic, oblong ovate to obovate in outline, rounded or acuminate to the obtuse apex; from the summit of the ovary, 2.3–4.5(–5.4) mm long, 1–2.3 mm thick just prior to anthesis. Ovary 1–2.2 mm long, 0.8–1.5 mm thick at anthesis, broadly fusiform,

clavate, obovoid to subglobose, densely covered with soft, translucent, uncinate hairs. Floral tube 0.4–2.4 mm long, 0.1–0.3 mm thick at the narrowest point, linear obtriangular to funnelform in outline, often with short glandular hairs evenly distributed on the surface. Sepals 1.3–3.8(–4.5) mm long, 0.8–2.4 mm wide, densely to sparsely pubescent or glabrescent on the abaxial surface with hairs as on the buds; pale green or purple; very broadly elliptic, oblong to ovate, abruptly short acuminate to the obtuse or subacute apex, reflexed in flower. Petals 1–3.7 mm long, 1.4–3.4(–4) mm wide, more commonly wider than long, white or pink, broadly deltoid to broadly obovate or depressed broadly obovate in outline, obcordate; the apical notch 0.4–2(–2.4) mm deep, ⅓ to slightly over ½ the length of the petal. Stamens normally spreading at anthesis, shorter than, or equal to, rarely longer than the style; filaments (1.2–)1.8–3.5(–4.3) mm long; anthers 0.3–0.8(–1) mm long, 0.3–0.9 mm thick. Style erect, straight or slightly drooping at the tip, 1.8–5.5(–6) mm long, topped by an obconic, obtriangular or narrow, transversely oblong, scarcely to prominently bilobed stigma, 0.2–0.4(–0.6) mm tall, 0.3–0.9 mm thick. Nectar secreting disc conspicuous and exserted beyond the opening of the floral tube, 0.2–0.7 mm tall, 0.3–1.1 mm thick, cylindrical, occasionally dilated at the apex. Mature fruit 2.2–3.9(–4.5) mm long, 1.4–3.6 mm thick, clavate, obovate, pyriform to subglobose, narrowly to broadly rounded at the apex, tapering smoothly or obliquely rounded to the pedicel; bilocular and 2-seeded, with or without prominent ribs and sulci, densely covered with stiff, translucent, uncinate hairs, 0.7–1.2 mm long and with short, capitate and clavate-tipped, glandular hairs ca. 0.1 mm long. Fruiting pedicels recurved to reflexed, often sharply so. Combined length of pedicel and mature fruit, (4.3–)6.3–11(–15) mm long. Gametic chromosome number, $n = 11$.

Distribution: Cool temperate deciduous forests. Europe and North Africa to southwestern Asia and from the European part of the Soviet Union to central Far Eastern Asia; eastern, southeastern and central North America. From near sea level to ca. 2,200 m. Flowering, June to late August and sporadically to early September.

Circaea lutetiana is treated here as being composed of three subspecies, *lutetiana*, *canadensis*, and *quadrisulcata*, occurring in three more or less isolated regions of the northern hemisphere, Europe, and North Africa to southwestern Asia; eastern North America; and eastern Europe from the vicinity of Moscow eastward between 50° and 60° N. Lat. to Far Eastern Asia.

Circaea lutetiana subspp. *canadensis* and *quadrisulcata* are obviously more closely related to each other than either is to subsp. *lutetiana*. *Circaea lutetiana* subspp. *canadensis* and *quadrisulcata* exhibit the classical pattern of disjunction between eastern North America and Asia (Fernald, 1915; Hara, 1939, 1952) although the Asian plants are not restricted to the eastern part of the continent as previously thought (Hara, 1952).

Although subspp. *canadensis* and *quadrisulcata* are placed in *C. lutetiana*, this might not ultimately prove to be the best treatment. I have combined the three subspecies on the basis of information provided by A. K. Skvortsov and P. H. Raven (pers. comm.), who maintain that *C. lutetiana* subsp. *lutetiana* and subsp. *quadrisulcata* intergrade in the European part of the Soviet Union and on

the fact that specimens of subsp. *lutetiana* from that region tend to be nearly glabrous whereas specimens of subsp. *quadrisulcata* from the same region tend to have more pubescent stems than plants from the eastern part of the range. Mature fruits, which are very different in the two subspecies and critical for identification, are, unfortunately, usually lacking on specimens that I have seen from this area of overlap. Extensive field studies by those in a position to do so are necessary to definitely resolve this situation. Specimens that appear to be intermediate between *C. lutetiana* subspp. *lutetiana* and *quadrisulcata* are listed following the specimens examined of subsp. *lutetiana*.

Circaea lutetiana subsp. *canadensis* and subsp. *quadrisulcata* are very similar and can be separated only using cryptic characters. The North American subsp. *canadensis* is generally larger in all floral parts than its Asian counterpart and nearly always has a minute bracteole at the base of the pedicel that is always lacking in *C. lutetiana* subsp. *quadrisulcata*. Hara (1952), in addition to the bracteole difference, also mentions that plants from North America commonly have green sepals and white petals while the Asian plants tend to have purple sepals and pink petals. The difference in color is unreliable and cannot be used diagnostically.

Mature fruits of *C. lutetiana* subspp. *canadensis* and *quadrisulcata* are pyriform to subglobose and have prominent, corky thickened ribs and deep sulci. Fruits of the North American subsp. *canadensis* are slightly larger. In contrast, the fruits of *C. lutetiana* subsp. *lutetiana* are obovoid to clavate and the longitudinal corky thickenings are either highly reduced or absent. Sulci are also lacking on the fruits of subsp. *lutetiana*. Specimens with immature fruit from the critical area of overlap of *C. lutetiana* subspp. *lutetiana* and *quadrisulcata* in European Russia tend to have the immature fruits flattened in pressing, obscuring the differences in morphology. *Circaea lutetiana* subsp. *lutetiana* also differs from subsp. *quadrisulcata* in other, more subtle ways. The floral tube in *C. lutetiana* subsp. *lutetiana* is almost always longer and more slender and the floral parts are generally larger than in subsp. *quadrisulcata*. In size of floral parts, *C. lutetiana* subsp. *lutetiana* compares favorably with subsp. *canadensis*.

KEY TO THE SUBSPECIES OF *CIRCAEA LUTETIANA*

a. Fruit pyriform to subglobose, with prominent ribs and deep sulci, tapering obliquely to the pedicel; stem commonly glabrous except for a few falcate hairs on the upper part; floral tube funnelform, 0.4–1.2 mm long.
  b. Pedicels with a minute bracteole 0.2–0.7 mm long at the base; plants of North America ..... 4a. subsp. *canadensis*
  b. Pedicels without a minute bracteole at the base or, if so, the bracteole less than 0.2 mm long; plants of east central Europe to Far Eastern Asia ..... 4b. subsp. *quadrisulcata*
a. Fruit clavate to obovoid, without prominent ribs and sulci, tapering smoothly to the pedicel; stem most commonly pubescent; floral tube very narrowly obconic to slender-funnelform, 0.8–2.4 mm long ..... 4c. subsp. *lutetiana*

4a. Circaea lutetiana L. subsp. **canadensis** (L.) Asch. & Magnus, Bot. Zeitung (Berlin) 28: 787. 1870.—FIG. 9.

Circaea lutetiana L. *β canadensis* L., Sp. Pl. 9. 1753.
Circaea latifolia Hill, Br. Herb. 138. 1756. Nom. illegit.
Circaea canadensis (L.) Hill, Veg. Syst. 10: 21. 1765.

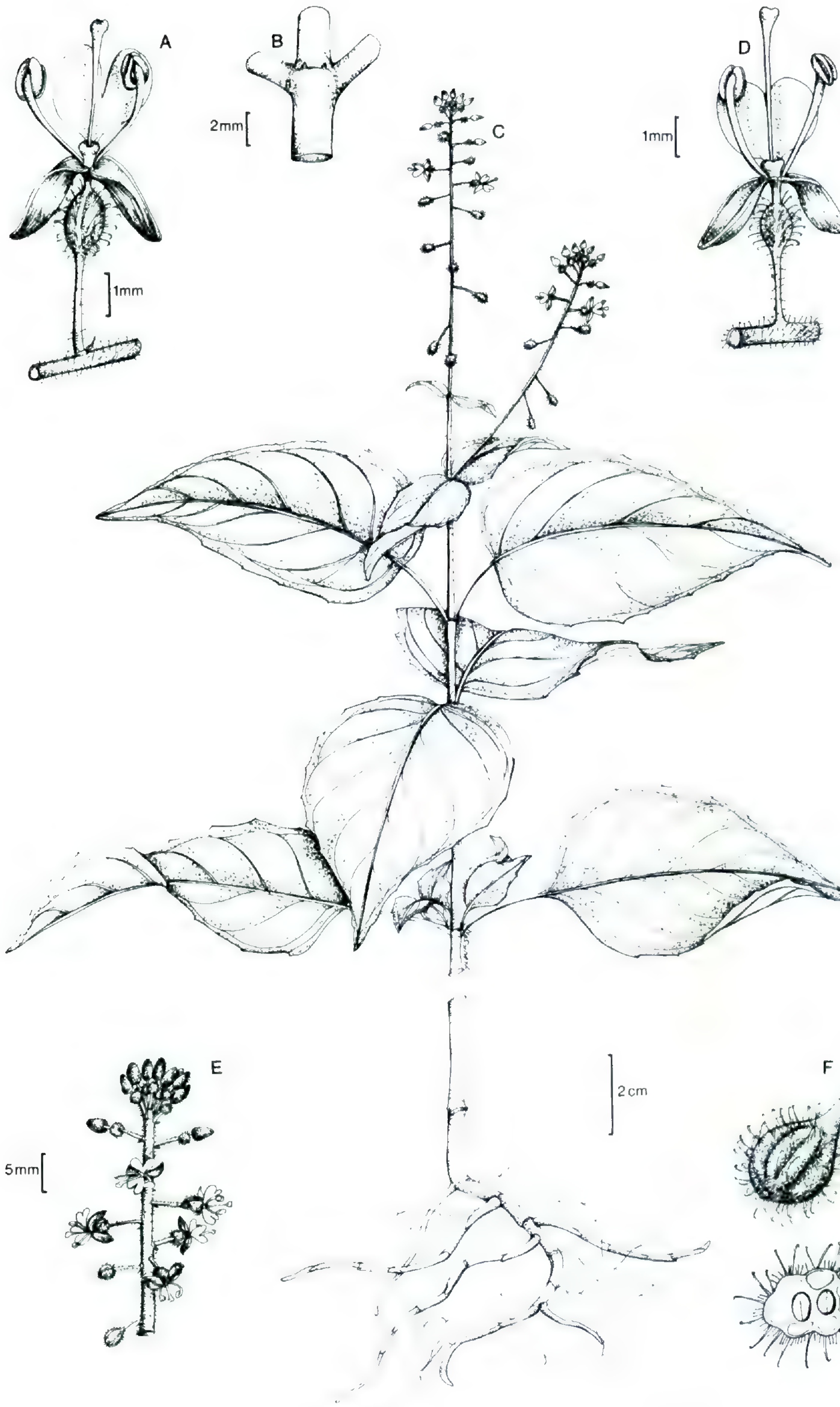


FIGURE 9. *Circaea lutetiana* L. subsp. *canadensis* (L.) Asch. & Magnus.—A. Flower with petal removed; note exserted nectary and bracteole at base of pedicel.—B. Upper node of stem.—C. Habit.—E. Inflorescence.—F. Fruit. After *Boufford 18828* (CM, KYO, MHA, MO, PE). *Circaea lutetiana* L. subsp. *quadrisulcata* (Maxim.) Asch. & Mag.—D. Flower with petal removed; note absence of bracteole. From *Boufford & Wood 19765* (KYO, MO, PE).

Circaea quadrisulcata (Maxim.) Franchet & Savat. var. *canadensis* (L.) Hara, Rhodora 41: 387. 1939.
Circaea canadensis (L.) Hill var. *virginiana* Fern., Rhodora 47: 161, *tab. 896, fig. 1–4*. 1945. TYPE: United States, Virginia, Brunswick County, Seward Forest near Triplett, 23 June 1944, *M. L. Fernald & J. B. Lewis 14643* (GH, holotype; GH, MO, NY, POM, US, isotypes).
Circaea quadrisulcata (Maxim.) Franchet & Savat. subsp. *canadensis* (L.) Löve & Löve, Taxon 31: 349. 1982.

Plants 1.2–9 dm tall. The stem glabrous, petioles, leaves and inflorescence pubescent as in the species but never with long, straight or slightly curved, patent hairs, 0.5–1 mm long. Leaves (5–)7–13(–16) cm long, (2.5–)3.5–6(–8.5) cm wide, narrowly to broadly ovate to, more commonly, oblong ovate. Petioles (1.3–)2.5–5.5 cm long. The terminal raceme ca. 2.5 cm long at initiation of flowering, to 30 cm long at cessation of flowering; the lateral racemes 2–5 cm long at initiation of flowering, to 20 cm long at cessation of flowering. Flowering pedicels 2–5(–6) mm long, with a minute, setaceous bracteole, 0.2–0.4(–7) mm long, at the base. Fruiting pedicels (3.5–)4–6.5 mm long. Buds (2.3–)3–4.1 mm long, (1.2–)1.5–2.3 mm thick just prior to anthesis, green or purple, especially towards the apex. Ovary 1.2–1.7 mm long, 0.8–1.3 mm thick at anthesis, obovoid to subglobose. Floral tube (0.4–)0.7–1.2 mm long, 0.2–0.3 mm thick at the narrowest point, funnelform. Sepals (1.9–)2.4–3.8 mm long, (1.2–)1.5–2.4 mm wide, very broadly elliptic, oblong to oblong-ovate, green or purple. Petals (1.3–)1.6–2.9 mm long, (1.5–)2.2–3.2(–4) mm wide, commonly white; the apical notch 0.4–1.7 mm deep, ⅓ to slightly over ½ the length of the petal. Filaments (1.2–)2–2.8 mm long; anthers 0.6–0.8 mm long, 0.5–0.8 mm thick. Style (2.5–)3.5–5.5 mm long; stigma 0.2–0.4 mm tall, 0.3–0.6 mm thick. Nectar secreting disc 0.2–0.7 mm tall, 0.5–1.1 mm thick. Mature fruit 2.8–3.9(–4.5) mm long, 1.9–3.6 mm thick, pyriform to subglobose, broadly rounded at the apex, rounded, usually obliquely, to the pedicel, with prominent ribs and deep sulci. Fruiting pedicels reflexed or recurved, often strongly so. Combined length of pedicel and mature fruit, 6.3–8(–11.2) mm long. Gametic chromosome number, $n = 11$.

TYPE: Sheet I: 26 in the Linnaean Herbarium at Stockholm (S) can be taken as the lectotype. The sheet has "*Circaea*" and "E Virginia" written in Linnaeus' hand on the front along with "*Circaea lutetiana* var. *canadensis*" by Wikström. The sheet is annotated on the back "Virginia" in Solander's hand and "*Circaea lutetiana β canadensis*" by Casström. The specimen was probably collected by Pehr Kalm, who collected in Virginia in the 1740s.

Distribution (Fig. 10): Widespread in eastern and central North America in cool temperate deciduous forests. From southern Georgia to west central Oklahoma, north to central North Dakota and southeastern Manitoba, eastward along the southern edge of the Canadian Shield to Quebec, Nova Scotia, and New Brunswick. Local in the southeastern, southern and western parts of the range. From sea level to 1,800 m. Flowering, (early-)mid-June to mid-August and sporadically to early September.

Representative specimens examined:

CANADA. MANITOBA: Roseisle, bord du ruisseau, *A. Champagne 22* (DAO); Lac du Bonnet, Stevenson's Point, *G. M. Keleher 363* (WIN); 9 mi. N of Rathwell, near the Assiniboine, *A. Champagne in 1946* (DAO). NEW BRUNSWICK: ALBERT COUNTY, Steeves-Hartley Bridge W of Hillsborough,

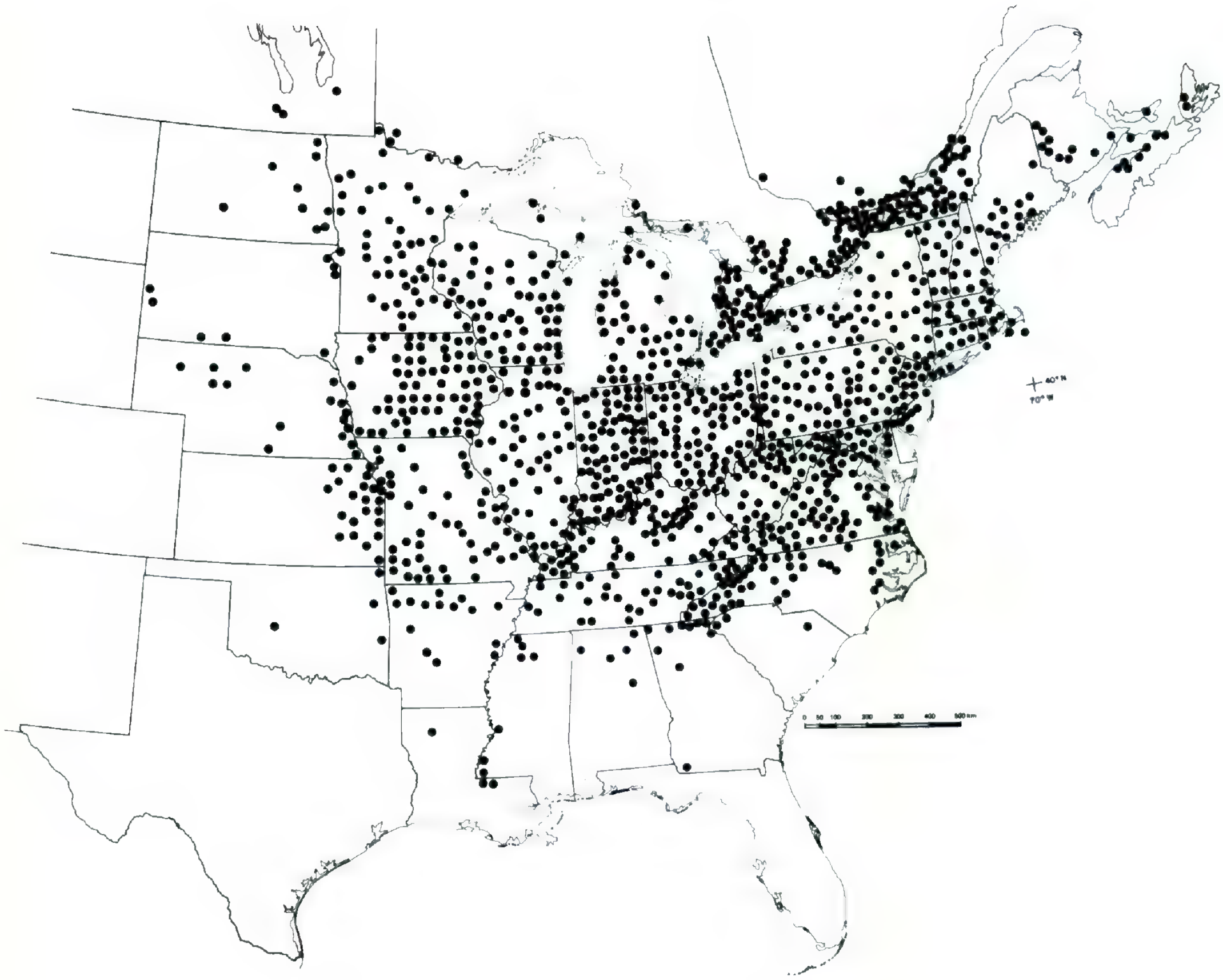


FIGURE 10. Distribution of *Circaea lutetiana* L. subsp. *canadensis* (L.) Asch. & Mag.

H. Scoggan & D. Erskine in 1955 (ACAD); CARLETON COUNTY, Woodstock, *M. L. Fernald & B. Long 14204* (CAN, GH, PH), Woodstock, ca. 15 mi. NW of town, *H. J. Scoggan 13567* (ACAD, MAK, W), Perth, N of Woodstock, by St. John R., *H. J. Scoggan 12659* (CAN), Hartland, *P. R. Roberts 60-266* (UNB), 2 mi. SE of Hartland, *E. Smith & R. Clattenburg 20012* (ACAD), 1 mi. E of Richmond Corner on Houlton Road, *P. R. Roberts & B. Pugh 65-412* (UNB), Island Park, *P. R. Roberts & D. E. Drury 63-1463* (DAO) *63-1462* (UNB), near Jackson Falls, E side of Meduxnekeag R., *K. Heinstein in 1965* (UNB), Jacksonville, Moody Hill, *D. Christie 2457* (DAO); KINGS COUNTY, no further data, *Britain in 1885* (CAN); YORK COUNTY, Nashwaak, Nashwaak R., *M. L. Fernald & A. S. Pease 25203* (CAN, GH, MT, NY, US), near Parcut Ferry, N side of St. John R., *K. Heinstein in 1965* (UNB), Keswick, *P. R. Roberts 59-969* (UNB), in woods near Keswick, *E. Smith 19304* (ACAD, CAN), Queensbury, *V. Dippitt 799* (UNB), Dumfries, *W. A. Squires in 1963* (DAO). NOVA SCOTIA: COLCHESTER COUNTY, near Truro, *A. R. Prince & C. E. Atwood 1410* (DS, MICH); CUMBERLAND COUNTY, New Prospect, *W. B. Schofield 3419* (ACAD, CAN, DAO); HANTS COUNTY, Five Mile R., *A. S. Pease & B. Long 22003* (GH, PH), Upper Kennetcook, Lattie's Brook, *J. & D. Erskine 55576* (ACAD), Halfway R. above Hantsport, *J. S. Erskine 53293* (ACAD, DAO, TRT); INVERNESS COUNTY, Melford, *E. C. Smith et al. 8729* (ACAD, CAN, DAO, MT, TRT), Hillsborough, *E. C. Smith et al. 4838* (TRT) *999* (ACAD, DAL); KINGS COUNTY, Cape Blomidon, *W. B. Schofield 5225* (ACAD, CAN, DAO, MT, TRT), above White Rock, *J. S. Erskine 541175* (ACAD), Cambridge, Cornwallis R., *W. B. Schofield 77* (ACAD, DAL), above Cambridge Station, *J. S. & D. S. Erskine 50427* (DAL, DAO); PICTOU COUNTY, Intervale woods, Middle R., *D. Sampson 119* (ACAD, MT), West R., *E. C. Smith et al.* (ACAD). ONTARIO: ALGOMA DISTRICT, Prince Township, Gros Cap, *S. Losee 2512* (H); BRANT COUNTY, Brantford Township, Whiteman's Creek, *W. H. Minshall 3908* (DAO), Spottiswood Lake, 10 mi. S of Galt, *B. C. Frankton et al. 655* (DAO); BRUCE COUNTY,

Kincardine Township, Tiverton, *P. F. Maycock & A. Auclair 9140* (MIN, MTMG), Carrick Township, 3 mi. NW of Lakelet, *G. R. Thaler 399* (TRT), Eastnor Township, ca. 2 km NW of Hope Bay, *D. G. Cuddy & G. McConachie 1850* (CAN), near Kemble, *H. Reeves in 1951* (TRT), Carrick Township, 1 mi. N of Belmore, *G. R. Thaler 397* (TRT); CARLETON COUNTY, Brittonia Park, *A. W. Anderson in 1945* (CAN), *Fr. R. Germain 1272* (CAN, TRT), Carsonby, 2 mi. N of N Gower, *J. Op de Beeck in 1968* (MTMG), Gloucester Township, *W. H. Minshall 3323* (DAO), Fitzroy Township, *W. H. Minshall 3300* (DAO, RM), Nepean Township, Woodroffe, *W. H. Minshall 1821* (BH, DAO, MIN, NA, NY), Gloucester Township, Rideau R., *W. H. Minshall 294* (DAO, NA, NY), Osgoode Township, 2 mi. SW of Manotick Station, *W. G. Dore 14379* (DAO), Ottawa, Dow's Swamp, *L. Jenkins 3050* (DAO, W), Riopelle Island, Ottawa R., *H. Groh 5203* (CAN), Beechwood, *J. M. Macoun in 1891* (TRT), Cunningham Island, Ottawa R., *H. Groh 5389* (CAN, DAO) *W. F. Reeve 6561* (UBC); DUFFERIN COUNTY, 2.5 mi. N of Orangeville, *G. R. Thaler 277* (TRT), 0.25 mi. S of Terra Nova, *W. J. Cody 21429* (DAO); Durham County, Cartwright Township, 3 mi. NE of Blackstock, *E. Haber 539* (CAN, DAO, MTMG, TRT); ELGIN COUNTY, Port Stanley, *W. J. Cody 1956* (DAO), Yarmouth Township, near St. Thomas, *L. E. James in 1950* (DAO), 5 mi. SE of St. Thomas, *L. E. James 1791* (DAO, DUL, MT, TRT, W), 1 mi. W of Port Bruce, Lake Erie, *H. A. Senn 3265* (DAO, TRT), 4 mi. N of Dutton, *J. H. Soper & H. M. Dale in 1948* (TRT); Essex County, Sandwich W Township, 1 mi. E of LaSalle, *J. K. & M. E. Shields 1395* (CAN, TRT) *1471* (ACAD, HAM, TRT), Sandwich S Township, 4 mi. from central Windsor, *J. K. & M. E. Shields 1372* (HAM, TRT), Gosfield S. Township, 4.25 mi. SW of Kingsville, *J. K. Shields & J. H. Soper 1431* (TRT), 4 mi. NW of Kingsville, *J. K. & M. E. Shields 1444* (ACAD, MIN, TRT), S side of Windsor, *W. G. Dore & C. J. Marchant 2409* DAO); FRONTENAC COUNTY, Howe Island, *W. J. Cody & D. Munro 22471* (DAO, TRT), Milton Island, *W. J. Cody & D. Munro 22577* (DAO), ca. 3 mi. ENE of Kingston, *W. G. Dore 18099x* (DAO), 5 mi. W of Kingston, *W. G. Dore & J. W. Kemp 16771* (DAO), Kingston, *J. Fowler in 1893* (MO) *in 1897* (US), Loughborough Township, Upper Rock Lake, *J. M. Gillett 6568* (DAO, MIN, NY, TRT), Frontenac Park, 1 km W of Salmon Lake, *R. Hainault & I. Macdonald 5146* (CAN, H, SASK), Cartwright's Point, Kingston, *E. Leach 420* (TRT), 7 mi. below Kingston, *F. W. Pennell 16286* (PH); GATINEAU COUNTY, Hull Township, Tenaga, *R. L. Gutteridge 903* (DAO), Gatineau Park, E of Ridge Road, *H. A. Senn et al. 1034* (DAO, WIS) *1033* (MO), Gatineau Park, Eardley Township, *J. M. Gillett 730* (DAO, UTC); GLENGARRY COUNTY, Colquhouns Island, *G. N. Gogo 472* (DAO); GRENVILLE COUNTY, Prescott, 1.8 mi. W of center of town, *W. G. Dore & J. M. Gillett 18068* (DAO), 2 mi. N of Prescott, *W. G. Dore et al. 18050* (DAO), 3 mi. SW of Prescott, *W. G. Dore* (DAO); GREY COUNTY, Jones Falls, W of Owen Sound on Hwy 6, *D. E. Boufford 18814* (BM, CM, G, K, KYO, MHA, MO, P, S), Holland Township, W of Arnott, *J. G. Grevatt 134* (TRT), Meaford, *W. Mauger 108* (MT); HALDIMAND COUNTY, Moulton Township, 2 mi. E of Dunnville, *B. Miller 428* (HAM), Port Dover district, *H. J. Scoggan 14180* (TRT); HALIBURTON COUNTY, Stanhope Township, Carnarvon, *V. Connolly 447* (TRT), Guilford Township, *E. & E. Sketton 452* (TRT); HALTON COUNTY, Nassagaweya Township, ca. 1.5 mi. N of Campbellville, *P. M. Catling & K. L. McIntosh in 1974* (TRT), Lake Crawford, *W. F. Grant 21* (HAM), near Hamilton, Waterdown, *J. H. Soper 950* (TRT); HASTINGS COUNTY, no further data, *J. Macoun in 1871* (MTMG), Marmora Township, Crowe Lake, *J. M. Gillett 7456* (DAO); HURON COUNTY, Clinton, *A. Cosens in 1900* (TRT), 10 mi. S of Clinton, *J. B. Phipps & J. B. Smith 3921* (TRT), Hullett Township, 2.5 mi. SE of Londesborough, *G. R. Thaler 177* (TRT), Tuckersmith Township, 2.5 mi. W of Seaforth, *G. R. Thaler 178* (TRT), Grey Township, Brussels, 5.5 mi. NE, *G. R. Thaler 228* (TRT), Stephen Township, 3 mi. S of Dashwood, *G. R. Thaler 252* (TRT), Usborne Township, 3 mi. N of Kirkton, *G. R. Thaler 252a* (TRT), Tuckersmith Township, 3 mi. NE of Hensall, *G. R. Thaler 275* (TRT), Stanley Township, 5 mi. NW of Hensall, *G. R. Thaler 300* (TRT), 4 mi. NW of Zurich, *G. R. Thaler 308* (TRT), McKillop Township, 1.5 mi. NE of Seaforth, *G. R. Thaler 408* (TRT), 4 mi. N of Seaforth, *G. R. Thaler 412* (TRT), Hay Township, 2 mi. SE of Zurich, *G. R. Thaler 421* (TRT), Goderich Township, 4 mi. N of Bayfield, *G. R. Thaler 440* (TRT); KENT COUNTY, Rondeau Park, *W. S. Dickinson 573* (CAN, DAO, TRT), Camden Township, 3 mi. S of Thamesville, *J. M. Gillett 16854a* (DAO, TRT), Rondeau Park, *R. W. Neal 358* (HAM), Rondeau Park, by Lake Erie, *H. J. Scoggan 14787* (CAN, TRT), Oxford Township, 1.5 mi. N of Clearville, *J. H. Soper & H. M. Dale 4091* (ACAD, DAO, GH, MIN, MO, MT, TRT); LANARCK COUNTY, 1.5 mi. E of Bathurst St., *R. A. Lubke 828* (TRT), Ramsay Township, Almonte, Lots 15 & 16, *W. H. Minshall 1740* (DAO); LEEDS COUNTY, Thwartway Island, *W. J. Cody & D. Munro 22378* (DAO), Grenadier Island, *W. J. Cody & D. Munro 22788* (DAO), Endymion Island, *W. J. Cody & D. Munro* (DAO), McDonald Island, *W. J. Cody & D. Munro 22508* (DAO), Gordon Island in the St. Lawrence R., *W. G. Cody et al. 19677* (DAO, TRT), Oliver's Ferry, *T. Edmonson in 1898* (NY), Crosby Township, Queen's Biological Station, Lake Opinicon, *J. M. Gillett 1468* (DAO), W Grenadier Island, *D. Munro 1* (DAO), Lake Opinicon, S Crosby Township, *J. Shields 569* (ACAD, TRT), near Chaffey's Locks, *R. Erskine 14962* (ACAD), Hay Island, Gananoque, *G. Kennedy in 1908* (GH); LINCOLN COUNTY, 2 mi. N of Queenston, *T. R. Davidson 115* (DAO), Niagra Township, 2 mi. SW of Queenston, *B. Miller 342* (HAM), near Jordan, *J. H. Soper & K. K. Shields 4882* (CAN, HAM, MO, MT, TRT),

Gananoque, *J. M. Stewart 58* (HAM), Jordan Harbour, *T. Taylor 73* (TRT); MANITOULIN DISTRICT, Kagawong, between Bridal Veil Falls & Bay, *K. Winterhalder 8580* (CAN); MIDDLESEX COUNTY, London, *T. J. W. Burgess in 1878* (MTMG), *T. J. W. Burgess in 1879* (US), *T. Millman in 1879* (TRT), Univ. of W Ontario, *G. F. Ledingham 5643* (USAS), *W. H. Minshall 4465* (DAO), Glencoe, *N. D. Keith in 1893* (MTMG), 3 mi. SE of Granton, *J. K. Shields 155* (TRT), 1.5 mi. SW of Granton, *G. R. Thaler 285* (TRT), 2 mi. NW of Iderton, *G. R. Thaler 287* (TRT), 2.5 mi. N of Lobo, *G. R. Thaler 289* (CAN, TRT), 4 mi. N of Lucan, *G. R. Thaler 387* (TRT), Strathroy, *G. M. Stirrett 1497* (DAO); MUSKOKA COUNTY, Port Carling, *L. E. Coleman in 1938* (TRT), 1.75 mi. NE of Kilworthy Station, *R. E. Whiting 758* (TRT), Benusoleil Island, Frying Pan Bay, *G. R. Thaler 337* (TRT); NORFOLK COUNTY, Port Royal, S Walsingham Township, *J. E. Cruise 5099* (BH, CAN, TRT), Woodhouse Township, Marlburg, *J. E. Cruise 9853* (TRT), Long Point, Lake Erie, *J. B. Falls & W. L. Klawe 655* (TRT), Charlotteville Township, Lot 18, *M. Landon 494* (HAM), 2 mi. N of Middleton, *P. F. Maycock & O. B. Maryniak 6221* (MTMG), Turkey Point, Lake Erie, *W. M. Bowden in 1935* (HAM), *H. J. Scoggan 14907* (CAN), *J. H. Soper 288* (TRT), 4 mi. SW of Tillsonburg, *W. Stewart 1016* (DAO); NORTHUMBERLAND COUNTY, Presqu'ile Pt. Provincial Park, *M. G. Dumais 398* (TRT); ONTARIO COUNTY, 2.5 mi. N of Leaksville, *P. M. Catling & S. McKay in 1970* (TRT), 6 mi. W of Enniskillen, *L. Gad et al. in 1974* (TRT), Swiss Chalet Park, *E. Haber 557* (DAO, MTMG, NCU, TRT), Uxbridge Township, 1 mi. SE of Sky Lodge, *M. Heimburger in 1950* (TRT), Rouge R., *J. L. Riley in 1973* (TRT), Scolasticat St. Joseph, *R. Gilbert 21* (DAO); OTTAWA-CARLETON COUNTY, Billing's Bridge, *W. H. Minshall in 1933* (DAO), N Gower, *J. M. Wallace s.n.* (SASK), Rockcliffe Park, Ottawa, *M. E. Forward in 1935* (UBC), *H. Lloyd in 1944* (CAN); OXFORD COUNTY, N Norwich Township, *T. Hinks in 1971* (TRT), 3 mi. W of Embro, *P. F. Maycock & O. B. Maryniak 6650* (MTMG), 3 mi. SE of Granton, *J. K. Shields 155* (CAN, HAM, MO, MT), N Norwich Township, *L. Stock in 1954* (TRT), 6 mi. N of Embro, *G. R. Thaler 380* (TRT), 3 mi. from Ingersoll, *G. R. Thaler 383* (TRT), end of Sunova Lake, *G. L. Thaler 404* (TRT), 4 mi. SW of Hickson, *G. R. Thaler 406* (TRT), 2 mi. NE of Innerkip, *G. R. Thaler 436* (TRT); PAPINEAU COUNTY, Templeton Parish, *J. A. Calder M-137* (DAO); PARRY SOUND DISTRICT, Big Island, *E. McDonald 562* (US); PEEL COUNTY, Credit Forks, *H. H. Brown in 1929* (TRT, UBC), 3 mi. NE of Brampton, *P. F. Maycock & B. W. Davies 11423* (MTMG), Chinguacousy Township, *H. Saifu et al. in 1974* (TRT), Caledon, *M. Vickers 67* (TRT), Snelgrove, *J. White in 1908* (TRT); PERTH COUNTY, Elma Township, 3 mi. S of Listowel, *G. R. Thaler 170* (TRT), Wallace Township, 2 mi. E of Listowel, *G. R. Thaler 173* (TRT), 3 mi. S of Palmerston, *G. R. Thaler 181a* (TRT), 3 mi. N of Motherwell, *G. R. Thaler 254* (TRT), 1 mi. E of Fullarton, *G. R. Thaler 259* (TRT), 2.5 mi. NE of Staffa, *G. R. Thaler 271* (TRT), 1.5 mi. NE of Granton, *G. R. Thaler 386* (TRT), 1 mi. N of Kinkora, *G. R. Thaler 434* (TRT), 1.5 mi. SE of Avonton, *G. R. Thaler 435* (TRT), 2.5 mi. S of Brodhagen, *G. R. Thaler 458* (TRT); PETERBOROUGH COUNTY, Sandy Lake, *J. E. Cruise 101* (TRT); PRESCOTT COUNTY, 4 mi. W of L'Original, *H. A. Senn 1614* (DAO, MT, NY), 3–6 mi. SE of Hawksbury, *W. H. Minshall 1496* (DAO); PRINCE EDWARD COUNTY, Picton, *J. Macoun 673* (GH), Rainy River District, SE corner of Basswood Lake, *C. E. Garton 4919* (DAO, MT, TRT), 4 mi. SW of Sleemans, *C. E. Garton 8886* (DAO, UC), Lake of the Woods Provincial Park, McCrosson Township, *C. E. Garton 9166* (DAO, MIN, SASK, TRT), 2.5 mi. below Rainy River Town, *C. E. Garton 9389* (DAO, MAK, UBC); RENFREW COUNTY, 2 mi. E of Renfrew, *B. Boivin & L. J. van Rens 14306* (DAO), 2 mi. W of Renfrew, *J. H. Soper 9345* (TRT), Haley Station, *T. Edmonson 2597* (NY); RUSSELL COUNTY, Casselman, *J. Macoun 2018* (CAN); SIMCOE COUNTY, Lake Simcoe, DeGrasse Point, *C. E. H. 108* (TRT), Midland, *T. M. C. Taylor 8379* (TRT), Minesing Swamp near Barrie, *S. Walshe 238* (CAN, DAO, TRT); STORMONT COUNTY, Sheek Island, Ault Park, *J. M. Gillett & W. G. Dore 7648* (ACAD, DAO, NCU), Steen Island, St. Lawrence R., *J. M. Gillett 7700* (DAO, TRT), 2 mi. NE of Wales, *J. M. Gillett 7746* (DAO, MT), 2 mi. W of Cornwall, *J. Op de Beeck in 1968* (MTMG), 2 mi. NW of Maxville, *M. J. Shchepanek & A. Dugal 1546* (CAN), Newington, *J. H. Lemon in 1895* (UBC); VICTORIA COUNTY, 3 mi. W of Norland, *W. J. Cody & J. A. Parmelee 6666* (DAO), 0.5 mi. E of church in Dalrymple, *W. S. Dickinson 414* (CAN, DAO, MTMG, NCU, TRT); WATERLOO COUNTY, Galt, *W. Herriot in 1910* (CAN, DAO, MT, TRT), Hamburg, *H. L. Merner in 1897* (WIS), German Mills, Cressman's Woods, *E. L. James 264* (HAM), 3 mi. NE of Linwood, *G. R. Thaler 295* (TRT), 3 mi. SW of Elmira, *G. R. Thaler 298* (TRT), Waterloo, *P. Hayne in 1973* (VDB), Kitchener, *G. R. Thaler 363* (TRT); WELLAND COUNTY, Bertie Township, Bowen Road, *B. Miller 213* (HAM, TRT), Niagra, *W. J. Potter in 1908* (TRT), Niagra Falls, *J. Macoun 44424* (GH), Niagra Gorge, *B. Miller 456* (DAO, HAM), 8 mi. W of Welland, *D. R. Lindsay 236* (DAO), 4 mi. NE of Winger, *L. C. Sherk et al.* (DAO); WELLINGTON COUNTY, Guelph, *H. Hood in 1956* (SASK), *J. J. Stroud in 1937* (TRT); WENTWORTH COUNTY, Red Hill, *R. S. Maines 80* (HAM), 2.5 mi. SW of Freelton, *S. J. Ives 74* (CAN, TRT), Cootes Paradise, Royal Botanical Garden, *J. B. Lord 47a* (HAM), 0.5 mi. S of Winona, *P. F. Maycock & O. B. Maryniak 1868* (MTMG), Hamilton, Dundas Marsh, *W. W. Judd 141* (HAM), Hamilton, *J. A. Riddell 54* (HAM), Hamilton, Sassafras Point, *F. Caesar 227* (HAM); YORK COUNTY, Concord, *H. H. Brown in 1928* (TRT), Pottageville, *H. H. Brown 4205* (TRT, UBC), Toronto, Serena Grundy Park, *E. Haber 540* (CAN, TRT), ca. 3 mi.

NE of King, *E. Haber 542* (CAN, DAO, MTMG, TRT), ca. 3 mi. NW of Nobleton, near Bolton, *E. Haber 554* (CAN, DAO, MTMG, NCU, TRT), ca. 1.5 mi. SW of Happy Valley, *D. Hoy et al. in 1977* (TRT), Toronto, local woods, *L. T. Owens in 1947* (TRT), Scarborough Township, *W. W. Robbins in 1908* (DAO), 1.5 mi. NW of Aurora, *J. K. Shields 899* (CAN, TRT), 3 mi. E of Kleinburg, *J. H. Soper & H. M. Dale 4133* (DAO, GH, MIN, MO, MT, TRT, US), near Pottageville, *W. R. Watson 2744* (TRT), Islington, *H. E. Welch 96* (DAO). PRINCE EDWARD ISLAND: Savage Harbour, *J. S. Erskine 00167* (ACAD). QUEBEC: ARGENTEUIL COUNTY, vicinity of Chatam, St. Phillipe d'Argenteuil, *J. B. McConnell in 1870* (MTMG), Calumet, *F. Adrien 1299* (MT), Chatham Township, between Cushing & Ottawa R., *L. Jenkins 7296* (DAO, WIN); ROBERT BALDWIN COUNTY, Pierrefonds, Cap St. Jacques, *E. Parnis 1522* (MTMG); BEAUHARNOIS COUNTY, Valleyfield, *A. Vezina V-4* (DAO), Ile Hébert in St. Lawrence R., *A. Bouchard & M. C. Herbert 2154* (MTMG); BEAUHARNOIS & CHATEAUGUAY COUNTIES, Iles de la Paix, Ile Lucas, *M. Morency 1355* (MT), Ile a Thomas, *M. Morency 1038* (MT), Ile du Large, *M. Morency 786* (MT), Ile a Tambault, *M. Morency 956* (MT); BELLECHASSE COUNTY, Vallier, pointe Amos, *Y. Desmarais 1180* (CAN, MTJB), St. Valier, *J. Cayouette 1172* (H); BROME COUNTY, Brome Mt., *A. Walther & A. Auclair in 1962* (MTMG), *A. Walther in 1962* (MTMG); CHAMBLY COUNTY, near Longueuil, *M.-Victorin 11269* (MT, WS), Chambly, *Fr. Cleonique 4274* (DAO, MT), *Fr. David in 1932* (MT), St. Bruno, *C. Morin 201* (MT); COMPTON COUNTY, Chartierville, *A. Roy 598* (MT); Deaux Montagnes County, Ste. Scholastique, *D. E. Swales 3750* (MTMG), near St. Jerome, *M.-Victorin 11270* (MT, PH), Ste. Placid, *M.-Victorin et al. 2059* (DAO, W, MT), Oka, *J. R. Beaudry 58-223* (MT), La Trappe, *P. Louis-Marie 24083* (MT); DRUMMOND COUNTY, 6.5 mi. NW of Richmond, *G. & P. H. Du Boulay 1039* (MTMG), 2 mi. W of Ste. Felix de Kingsey, *S. Brisson 762036* (MTMG, NLU); FRONTENAC COUNTY, St. Hilaire, *H. H. Lyman in 1877* (MTMG); GATINEAU COUNTY, Mont Ste. Marie, *W. G. Dore & F. J. Beales 22503* (MTMG), Wakefield, *J. Macoun 59938* (CAN), Blue Sea Lake, *A. E. Porsild 6361* (CAN), Meach Lake, *R.-Germain 6187* (CAN), *M. Malte 428/23* (CAN, W), *Br. Rolland 6187* (GH, MT), Hull, *J. Macoun in 1884* (NY), Gatineau Park, Skyline Trail, *H. A. Senn 2058* (DAO, RSA), E end of Ridge Road, *H. A. Senn et al. 1033* (DAO), Gatineau Park, *J. M. Gillett 14245* (CAN), Lake Gauvreau, *F. W. Pennell* 16553 (PH), Mont Ste. Marie, *W. G. Dore 22388* (DAO), Ironside, Gatineau valley, *M.-Victorin 15901* (GH, MT); HOCHELAGA COUNTY, Otremont Mt., *P. F. & T. Maycock 9332* (MTMG, NCU), Mont Royal Mt., *A. Walther & A. Auclair in 1962* (MTMG), Mont Royal, *E. Roy 2948* (DAO, MT), *M.-Anselme in 1931* (MT, UC); HULL COUNTY, Kingsmere, Skyline Trail, *I. & T. Owen 972* (DAO); HUNTINGDON COUNTY, Port Lewis, *A. Bouchard 67178* (CAN, MTMG), Ross Island, *G. N. Gogo 471* (DAO); IBERVILLE COUNTY, 2 mi. E of Iberville, *I. J. Bassett & A. Hamel 2457* (DAO), 1.5 mi. E of Ste. Gregoire, *I. J. Bassett & C. W. Compton 5563* (DAO), Mt. Johnson, *A. Walther in 1962* (MTMG); JACQUES CARTIER COUNTY, Senneville, *L. M. Terrill 2743* (MTMG), Valois, 1 mi. N of Lake St. Louis, *M. Jones 213* (MTMG), SW end of Ile St. Paul, *P. F. Maycock 7716* (MTMG); JOLLIETTE COUNTY, *A. Robert 325* (MT), St. Ambroise, *P. Louis-Marie & H. Dudemaine 1399* (CAN); LAVAL COUNTY, Laval Ouest, W from rte 8, *J. Op de Beeck in 1968* (MTMG); LEVIS COUNTY, Lauzon, behind Fort no. 1, *R. & R. Cayoutte 35-119* (OSC), Harlaka, *Fr. Michel 2278* (MT); LOUIS HÉBERT COUNTY, Laval, Univ. Laval, *J. G. Perras 70-321* (DAO, MAK); MEGANTIC COUNTY, Leeds Township, at Osgoode R. bridge, *J. A. Bailey 1623* (V); MISSISQUOI COUNTY, St. Armand, *M. Raymond & B. Boivin 1266* (DAO, MTJB, WIN), Philipsburg, *C. Knowlton in 1923* (GH, MO), Philipsburg Sanctuary, *A. Johnstone in 1963* (DAO, MTMG), *A. Pokorny in 1964* (MTMG); MONTMAGNY COUNTY, Ile aux Grues, *J. Rousseau 25249* (GH, MT, PH, US), Grosse Ile, *M.-Victorin et al. 40024* (MT), *R. P. Hanson 325* (DAO), *J. Sexsmith in 1944* (ALTA); MONTMORENCY COUNTY, St. Joachim, *V. Lavoie & D. Doyon 600803-10* (DAO), Ile d'Orleans, St. Famille, *B. Boivin et al. 60001* (CAN, MT, NY, WIS, WS), Ste. Pétronille, *D. Doyon DL610721-31* (DAO), Ile d'Orleans, *M.-Victorin 16176* (GH, MO, MT, POM, WS), Cap Tourmente, *M.-Victorin & R.-Germain 46511* (GH, MT), *M.-Victorin 15900* (MO, MT, NY, WS), SW end of Ile d'Orleans, *L. J. Uttal 11931* (VPI), Ange-Gardien, *V. Lavoie & D. Doyon 600712-11* (DAO); MONTREAL & JESUS ISLANDS COUNTY, Montreal, E. Rouleau *329* (MT), Beaconfield, *G. G. Campbell in 1892* (MTMG), Ile St. Helene, *E. Rouleau 1090* (MT), Ile Bizard, *C. Marcoux in 1940* (DAO); NICOLET COUNTY, Nicolet, *F. Stanislas 567* (MT), St. Sylvere, Maddington, *S. Brisson 68166* (CAN, CAS, DAO, H, MIN, TUR); PAPINEAU COUNTY, (Hull County?), Lake McGregor, *R. Gilbert 26* (DAO), 3 mi. NE of Poltimore, *M. J. Shchepanek & A. Dugal 984* (CAN), Buckingham, *R. Ross & E. Rouleau 7* (GH, MT); PONTIAC COUNTY, E of Shawville, *W. G. Dore 18422* (DAO), Onslow Parish, 1 mi. S of Wyman, *M. N. Zinck 856* (DAO); PORTNEUF COUNTY, Les Ecureuils, *D. Doyon & J. Deschenes 600725-04* (ACAD); QUEBEC COUNTY, Sillery, *C. Rousseau 63-1301* (DAO, MT, TRT, UBC, UC), Giffard, *D. Doyon D61071916* (TRT), Quebec, *P. L. Marie in 1929* (KYO), Parc du Pont, *R. Cayouette 46-7* (DAO), Cap Rouge, *Fr. Michel 1359* (MT); ROUVILLE COUNTY, Ile des Soeurs, Verdun, *S. Vincent in 1942* (MT), Rougemont Mt., *A. Walther & A. Auclair in 1962* (ACAD, MTMG, NY), Rougemont, *L. Cinq-mars et al. 65-115* (DAO, MAK), Mt. Yamaska, *Fr. Fabius 5532* (DAO), *A. Walther in 1962* (NY), Mt. St. Hilaire, *P. F. Maycock & O. B. Maryniak 3180* (CAN, DAO, MTMG, TRT), St. Hilaire, *M.-Victorin & R.-Germain 46801*

(DAO, GH, MT), Belsoeil Mt., *L. M. Terrill 1749* (MTMG); ST. JEAN COUNTY, St. Jean, *M. Raymond 9003* (MT); SHEFFORD COUNTY, Granby, *Fr. Fabius 331* (CAN, MT); SHERBROOKE COUNTY, 2 mi. N of Coaticook on hwy 22, *A. Bouchard et al. 69-651* (MTMG), city of Sherbooke, *S. Brisson 761016* (MTMG, NLU), *A. Legault 6528* (COLO, DAO, MTMG, TRT, UBC); Stanstead County, Lake Memphremagog, *J. R. Churchill in 1903* (MIN), Georgeville, *J. R. Churchill in 1902* (BH, GH, MO, MT), Libbyton, 4 mi. S of Ayers Cliff, *G. & P. H. Du Boulay 1305* (MTMG); TERREBONNE COUNTY, Rosmere, *E. Rouleau 733* (MT), Morris Island in R. des Milles Iles, *P. F. Maycock et al. 12463* (MTMG); TIMISKAMINGUE COUNTY, Lake Timiskaming, Ile du College, *W. K. W. Baldwin 5274* (CAN, MT, TRT); VAUDREUIL COUNTY, Ile Perrot, *D. E. Newton in 1931* (MTMG), Rigaud, *E. Roy 3245* (ACAD, CAN, MT, NY), *E. Roy 3907* (DAO, FSU, MT, PH, TRT), Rigaud Mt., Pitcairn's Pond, *D. E. Swales 3579* (MTMG), Rigaud Mt., Ranches Riding School, *A. Pokorny in 1963* (MTMG), Mt. Rigaud, *L. Newstrom 402* (MTMG).

UNITED STATES. ALABAMA: CULLMAN COUNTY, Hurricane Creek Park N of Cullman, *R. Kral 35373* (KANU, VDB); FRANKLIN COUNTY, vicinity of Russellville, *L. James 22* (MO); JACKSON COUNTY, under Porter's Bluff, *L. Porter in 1934* (GH); MARSHALL COUNTY, SSW of Guntersville along Big Spring Creek, *R. Kral 34822* (AUA, KANU, MO, VDB); TALLADEGA COUNTY, Salt Creek USDA Soil Conservation Service damsite no. 18, *R. C. Clark & T. A. Heard 2936b* (NCU). ARKANSAS: BENTON COUNTY, Cave Springs, *N. C. Fassett & E. L. Nielson 19793* (WIS); CRAIGHEAD COUNTY, vicinity of Monette, *D. Demaree 3327* (UARK); GARLAND COUNTY, Hot Springs, 20 mi. W on Cedar Glade Road, *F. J. Sculls 318* (POM); HOT SPRINGS COUNTY, Magnet Cove, *D. Demaree 19349* (MO, SMU); INDEPENDENCE COUNTY, P. O. Batesville, *D. Demaree 26729* (MIN, OKL, OKLA, RSA, STAR, RSA, UNA); IZARD COUNTY, approx. 8 mi. W of Cushman, *R. D. Thomas & J. Gray 9145* (NLU, WTU); LEE COUNTY, Mariana, Crowley's Ridge, *D. Demaree 12987* (DS, MO, NY, PH, SMU); LOGAN COUNTY, Magazine Mountain, *D. Moore 480343* (UARK); MADISON COUNTY, Withron's Springs, *J. T. Buckholz in 1923* (SMU, UARK, WIS); MARION COUNTY, Cotter, *E. J. Palmer 5944* (COLO, CU, H, MO, NDA, POM); NEWTON COUNTY, Terrapin Branch, Sect. 26, T14N, R23W, *P. L. Redfearn & W. Weber 27504* (NCU, UMO); PHILLIPS COUNTY, Helena, Crowley's Ridge, *D. Demaree 19009* (CAS, GH, ISC, MIN, MO, NY, SMU, UC); SEARCY COUNTY, 1 mi. W of U.S. 65 on Peyton Creek, *D. Lawson & Bio 451* (NLU); STONE COUNTY, 8 mi. N of Mountain View, *D. Moore in 1949* (UARK, WIS); WASHINGTON COUNTY, Natural Sidewalk, *D. M. Moore 470098* (WIS). CONNECTICUT: FAIRFIELD COUNTY, Orchard Point, Vaughn's Neck, Candlewood Lake, *F. C. Seymour 19921* (MO); HARTFORD COUNTY, Avon, along Farmington R., *F. C. Seymour 29818* (MO, NY); LITCHFIELD COUNTY, E of Salisbury, *D. E. Boufford & H. E. Ahles 18832* (KYO, MO); MIDDLESEX COUNTY, Haddam, Haddam Meadows, *F. C. Seymour 27440* (MO); NEW HAVEN COUNTY, Bethany, Bethany Bog, just NW of Bethany airport, *K. L. Chambers 1519* (DAO, DS, NCU, OSC, TUR, WS, WTU); NEW LONDON COUNTY, town of Franklin, *R. Woodward in 1906* (NEBC); TOLLAND COUNTY, Storrs, Mansfield Township, *M. Travis 2500* (NA, PENN); WINDHAM COUNTY, Killingly, *C. A. Weatherby 5853* (US). DELAWARE: NEW CASTLE COUNTY, near Centerville, *A. Commons in 1873* (PH). DISTRICT OF COLUMBIA: N of Washington, *S. F. Blake 6929* (LL). GEORGIA: DADE COUNTY, near Murphy Spring in Murphy Hollow, between Sand & Murphy Mts., *W. H. Duncan & H. Venard 13074* (GA); DECATUR COUNTY, woods, *J. P. Anderson in 1888* (MO); FANNIN COUNTY, N of Cooper Creek Recreation Area, *D. E. Boufford & E. W. Wood, 17303* (GA, NCU); FLOYD COUNTY, Marshall Forest, Rome, *H. R. DeSelm & L. Lepps 31393* (TENN); FULTON COUNTY, College Park, woods, *C. & D. P. Schallert 11080* (IDS, KANU); MURRAY COUNTY, Chattahoochee National Forest, Lake Conasauga Recreation Area, *H. G. DiGioia 143* (GA); RABUN COUNTY, near Tate City, *A. Cronquist 5549* (GA, GH, IND, MICH, MO, NY, PH, SMU, UC, US, WS); STEPHENS COUNTY, N of Toccoa, SW of Yonah Lake, *D. E. Boufford & E. W. Wood 16820* (NCU, UNCC, VSC); TOWNS COUNTY, N-facing ravine at Unicoi Gap, *W. H. Duncan 22373* (GA); UNION COUNTY, 3 mi. W of Vogel State Park, *J. W. Hardin 251* (GA, MICH). ILLINOIS: ALEXANDER COUNTY, Horseshoe Island, *G. N. Jones 12044* (ILL, NY, SMU); CASS COUNTY, Virginia, *F. C. Gates 61* (MICH); CHAMPAIGN COUNTY, 15 mi. W of Urbana, *G. N. Jones 16436* (ILL, MO, TEX); CHRISTIAN COUNTY, damp woods, *without collector in 1862* (LSU); COOK COUNTY, 3 mi. SE of Barrington, *N. R. Bennett 8512* (CM); CUMBERLAND COUNTY, 2 mi. W of Toledo, *J. C. Myers in 1950* (WVA); DEKALB COUNTY, no further data, *E. K. Abbott in July* (CAS); DUPAGE COUNTY, Naperville Park, *L. Umbach 6683* (MIN, NY, WS); FAYETTE COUNTY, NE of St. Elmo, *L. O'Dell 597* (ILL); FORD COUNTY, 0.5 mi. N of Roberts, *O. A. Seng 64* (ILL); GALLATIN COUNTY, Shawneetown, *E. J. Palmer 15497* (MO); HAMILTON COUNTY, Delafield Bottoms, *N. Tracy in 1972* (SIU); HANCOCK COUNTY, Hancock Township, Crooked Creek, *F. C. Gates 10035* (MO); IRIQUOIS COUNTY, E of Milford, *H. E. Ahles 3230* (ILL); JACKSON COUNTY, Grand Tower, *H. A. Gleason 2509* (GH); JERSEY COUNTY, Marquette Park, *P. Jacobs 14* (ILL); JO DAVIESS COUNTY, SW of Galena, *H. E. Ahles 4392* (ILL); JOHNSON COUNTY, 3 mi. S of Vienna, *J. White 1181* (NLU); KANE COUNTY, 7 mi. W of Aurora, *C. & E. Erlanson 1544* (NA); KANKAKEE COUNTY, SE side of Aroma Park, *D. Seigler & K. Becker 4936* (ILL); KNOX COUNTY, 4.5 mi. S of

Victoria, *J. C. Solomon 949* (KNOX, KYO, MO); LAKE COUNTY, 3 mi. S of Lake Zurich on U.S. 12, *D. Keil 532* (ASU); LASALLE COUNTY, Starved Rock, Illinois State Park, *F. H. Thone 12* (MO); LAWRENCE COUNTY, ca. 1 mi. W of Lawrenceville, *N. C. Henderson 66-634* (CAS, FSU, KANU); LEE COUNTY, Amboy, *J. B. Long 450* (ILL); MACON COUNTY, woods near Decatur, *H. A. Gleason 9151* (NY, WIS); MACOUPIN COUNTY, Rock House, *J. White 83* (SIU); MASON COUNTY, SE of Easton, *D. Seigler 7709* (ILL); MCDONOUGH COUNTY, near Lamoine R., *R. M. Meyers 4617* (NLU); MCHENRY COUNTY, Algonquin, *W. A. Nason in 1978* (ILL); MCLEAN COUNTY, 1.5 mi. N of McLean, *R. T. Calef 528* (ILL); MONROE COUNTY, NE¼, Sec. 13, T3S, R10W, *C. Bollwinkel 291* (SIU); MOULTRIE COUNTY, 2 mi. SE of Bethany, *R. P. Wunderlin & W. Chapman 329* (SIU); OGLE COUNTY, 6 mi. E of Polo, White Pine State Forest, *J. A. Steyermark 40719* (MO); PEORIA COUNTY, Kickapoo Valley, Horseshoe Bottom, *V. H. Chase 3149* (DS, IA, ILL, MICH, MIN, MO, NY, PAC, PH, POM, UC, US, WTU); PIATT COUNTY, near Monticello, *G. N. Jones 18946* (ILL); PIKE COUNTY, Shepherd, Mississippi bottoms, *J. Davis 4066* (MO); POPE COUNTY, Allen Hollow, *W. M. Bailey & J. R. Swayne 2515* (NCU); PUTNAM COUNTY, Putnam, *V. H. Chase 11245* (DUL, ILL); RICHLAND COUNTY, County Line Road, *R. Ridgway 3106* (PH, POM); SANGAMON COUNTY, 0.4 mi. S of the Sangamon R. on route I-55, *D. E. Boufford et al.* (G, MO, P); ST. CLAIR COUNTY, 4 mi. N of Millstadt, *D. Rhodes 729* (LTU); STARK COUNTY, Sec. 14, T12N, R6E, adjacent Spoon R., *R. Riggins 202* (UTC); TAZEWELL COUNTY, E Peoria, *V. H. Chase 11243* (DUL); UNION COUNTY, Panther's Den, *R. R. MacMahon 484* (MIN); VERMILION COUNTY, 5 mi. S of Potomac, *H. M. Franklin in 1949* (ILL); WABASH COUNTY, near Friendsville, *J. Schneck in 1879* (ILL); WASHINGTON COUNTY, Posin Road woods, *D. Windler 548* (SIU); WHITESIDE COUNTY, Sterling, Sinnissippi Park, *V. H. Chase 12914* (DAO, DS); WILL COUNTY, 2 mi. E of Braidwood, *Z. Vytanovych 4167* (UT); WINNEBAGO COUNTY, 2 mi. E of Harrison, *R. B. Anthony in 1935* (WIS). INDIANA: ADAMS COUNTY, 3.5 mi. W of Decatur, *C. C. Deam 40880* (IND); ALLEN COUNTY, along Cedar Creek, *C. C. Deam 14368* (IND); BLACKFORD COUNTY, ca. 2 mi. NE of Harford City, *C. C. Deam 61* (IND); BROWN COUNTY, Nashville, *J. Wright in 1892* (MIN, NDA); CARROLL COUNTY, ca. 7 mi. NE of Delphi, *C. C. Deam 17776* (IND); CASS COUNTY, Wabash River, 1 mi. above Georgetown, *R. C. Friesner 8840* (GA, UT); CLARK COUNTY, ca. 3 mi. NW of Henryville, *C. C. Deam 6940* (IND); CLAY COUNTY, ca. 2 mi. E of Harmony, *R. C. Friesner 21718* (SMU); CRAWFORD COUNTY, ca. 1 mi. NE of Leavenworth, *C. C. Deam 20412* (IND); DAVIESS COUNTY, 5 mi. NW of Odon, *C. C. Deam 25621* (IND); DEARBORN COUNTY, 3.5 mi. SE of St. John's Church, *R. C. Friesner 23448* (DAO, WIS); DEKALB COUNTY, ca. 2 mi. SE of Hamilton, *C. C. Deam 44932* (IND); DELAWARE COUNTY, ca. 2 mi. NW of Daleville, *R. C. Friesner 24273* (DUKE, LTU, OKL); DUBOIS COUNTY, ca. 1 mi. N of Jasper, *C. C. Deam 11571* (IND); ELKHART COUNTY, 3 mi. SE of New Paris, *C. C. Deam 50419* (IND); FAYETTE COUNTY, ca. 1 mi. SE of Alpine, *C. C. Deam 47300* (IND); FLOYD COUNTY, ca. 5 mi. SW of New Albany, *C. C. Deam 27921* (IND); FOUNTAIN COUNTY, Porlland Arch, *D. Siegler 7634* (OKL); FULTON COUNTY, ca. 8 mi. SW of Rochester, *C. C. Deam 64982* (IND); GIBSON COUNTY, ca. 6 mi. W of Patoka, *C. C. Deam 13356* (IND); GRANT COUNTY, E side of Dollar Lake, *Potzger 7019* (ND); GREENE COUNTY, ca. 5 mi. NE of Bloomfield, *C. C. Deam 44734* (CM, IND, UARK); HANCOCK COUNTY, near New Palestine, *Mrs. C. C. Deam 9094* (IND); HARRISON COUNTY, ca. 3 mi. SE of Elisabeth, *C. C. Deam 16387* (IND); HENDRICKS COUNTY, ca. 1.5 mi. W of Camby, *Mrs. C. C. Deam 11479* (IND); HENRY COUNTY, E side of Road 3, 0.6 mi. S of Road 40, *R. C. Friesner 24193* (SMU); HOWARD COUNTY, 3–4 mi. N and W of Kakoma, *C. Ek 46* (US); HUNTINGTON COUNTY, Salamonie Township, *C. C. Deam 2165* (IND); JACKSON COUNTY, 3 mi. SW of Brownstown, *R. Jackson 169* (IND); JASPER COUNTY, Barkley Township, *W. Welch 623* (ILL); Jay County, ca. 3.5 mi. NE of Pennville, *C. C. Deam 45138* (IND); JEFFERSON COUNTY, Clifty Falls State Park, *C. C. Deam 47500* (IND); JENNINGS COUNTY, ca. 0.5 mi. above Vernon, *C. C. Deam 11307* (IND); KNOX COUNTY, 1 mi. SE of Emison, *S. McCoy 4596* (DAO, UMO); KOSCIUSKO COUNTY, S of Warsaw, *F. Wann in 1917* (CU, PENN); LAGRANGE COUNTY, Wall Lake, along Ind. 120, *N. C. Henderson 61-570* (FSU); LAKE COUNTY, 3.5 mi. W of Lowell, *C. C. Deam 31621* (IND); LAPORTE COUNTY, 3 mi. NW of New Carlisle, *C. C. Deam 31409* (IND); LAWRENCE COUNTY, woods S of A. Cumming's house, *P. G. Wible 4550* (IND); MARION COUNTY, Indianapolis, 3700 block N Gladstone Ave., *R. C. Friesner 8799* (CAS, FUGR, OKLA, RM, SMU, TRT, WS); MARSHALL COUNTY, near Lake Maxinuckee, *J. Scovell & H. Clark 1274* (?) (US); MARTIN COUNTY, White R. ca. 1 mi. above Shoals, *C. C. Deam 11426* (IND); MIAMI COUNTY, 3 mi. W of Bunker Hill, *C. M. Ek in 1942* (MO); MONROE COUNTY, 10 mi. SE of Bloomington, *R. C. Friesner 3040* (ND); MONTGOMERY COUNTY, along Sugar Creek near the Shoals, *C. C. Deam 9329* (IND); MORGAN COUNTY, 2 mi. S of Morgantown, *R. C. Friesner 7581* (CAS, DUKE, OSC, PENN, POM, RM, SMU, TENN, TEX, TRT, UT, UTC, WVA); NOBLE COUNTY, E of Kendalville, *C. C. Deam 5153* (IND); OHIO COUNTY, ca. 3 mi. SE of Milton, *C. C. Deam 47406* (IND); OWEN COUNTY, 6.8 mi. SW of Whitehall, Green's Bluff, *S. I. Matsunami 178* (NCU); PARKE COUNTY, Turkey Run State Park, *R. F. Daubenmire in 1929* (WS); PERRY COUNTY, ca. 3 mi. N of the mouth of Deer Creek, *C. C. Deam 28517* (IND); PORTER COUNTY, Indiana Dunes State Park, along Dunes Creek, *H. R. Bennett 7068*

(OKL, W); POSEY COUNTY, Nash's Woods, *S. A. Cain in 1932* (TENN); PUTNAM COUNTY, ca. 20 mi. SW of Greencastle, Hoosier Highlands, *W. H. Welch 5939* (UC); RANDOLPH COUNTY, 2 mi. SW of Modoc, *C. C. Deam 41374* (IND); RIPLEY COUNTY, 1.5 mi. NW of Delaware P.O., *C. C. Deam 36997* (IND); RUSH COUNTY, 2 mi. W of Gowdy, *C. C. Deam 41413* (MT); ST. JOSEPH COUNTY, Notre Dame, *J. A. Nieuland 1873* (ND); SCOTT COUNTY, 2.5 mi. N of Lexington, *C. C. Deam 28014* (IND); SHELBY COUNTY, woods near Morristown, *Mrs. C. C. Deam 11335* (IND); SPENCER COUNTY, ca. 9 mi. N of Rockport, *C. C. Deam 25261* (IND); STEUBEN COUNTY, near Clear Lake, *C. C. Deam in 1904* (ISC, MO, US); TIPPECANOE COUNTY, Ross Biological Preserve, *C. W. Miller 207* (DUKE); UNION COUNTY, 1.6 mi. E of Fayette-Union County line at Road 44, *R. C. Friesner 20623* (MICH, MO, OKL, TEX); VANDENBURGH COUNTY, 5 mi. E of Evansville, *C. C. Deam 16779* (IND); VIGO COUNTY, Terre Haute, *B. Evermann in 1884* (US); WABASH COUNTY, ca. 4 mi. W of LaFontaine, *C. C. Deam 50315* (IND); WARREN COUNTY, 1.25 mi. S of Rainsville, *C. C. Deam 50625* (IND); WARRICK COUNTY, 2 mi. N of Yankee town, *C. C. Deam 25327* (MT); WASHINGTON COUNTY, home woodlot, *J. S. Brooks in 1929* (IND); WAYNE COUNTY, Williamsburg, *F. W. Pennell 9831* (MIN); WELLS COUNTY, Kemp's Woods in Harrison Township, *C. C. Deam 2327* (MIN); WHITE COUNTY, just W of Buffalo, *C. C. Deam 39406* (IND); WHITLEY COUNTY, ca. 3 mi. E of Columbia City, *C. C. Deam 45033* (UARK). IOWA: ADAIR COUNTY, no further data, *J. E. Gow in 1900* (IA); ALLAMAKEE COUNTY, Hanover Township, *W. L. Tolstead in 1933* (COLO); APPANOOSE COUNTY, NW of Unionville, *B. Shimck in 1902* (ISC); BLACK HAWK COUNTY, Cedar Heights, *M. Burk 618* (ILL); BOONE COUNTY, Des Moines River bottom, *D. Isely 4741* (OKLA, US); BREMER COUNTY, near Waverly, *B. Shimck in 1898* (ISC); BUCHANAN COUNTY, Winthrop, *M. Murley 1492* (ISC); CASS COUNTY, Cass Township, Sec. 15, SW¼, *C. P. Malone 371* (ISC); CEDAR COUNTY, 1 mi. SE of Rochester, *M. Fay 666* (OSC, UC); CERRO GORDO COUNTY, Mason City, SW side of Buffalo Slough, *B. Shimck in 1920* (IA); CHEROKEE COUNTY, Stiles property, *J. L. Carter 3095* (IA); CHICKASAW COUNTY, no further data, *W. D. Spiker in 1926* (ISC); CLARKE COUNTY, Osceola, *F. C. S. in 1892* (ISC); CLAY COUNTY, Little Sioux River in Wanata State Park, *A. Hayden 4000* (ISC); CLAYTON COUNTY, near McGregor, *G. J. Goodman 2700* (OKL, TEX); CLINTON COUNTY, Liberty Township, *T. S. Cooperrider 1805* (IA); DALLAS COUNTY, Des Moines Township, Des Moines R., *T. van Brugger 686* (IA); DAVIS COUNTY, Lick Creek Township, *A. Hayden 9170* (GH, ISC); DECATUR COUNTY, below spillway of lake in Nine Eagles State Park, *T. van Brugger 2577* (IA, SDU); DELAWARE COUNTY, Union Township, *M. D. Rickey 851* (IA); DES MOINES COUNTY, Flint Hills State Park, *C. L. Gilly 2819* (ISC); DICKINSON COUNTY, 2 mi. W of Milford, Little Sioux R., *R. F. Thorne 13218* (IA, UC); DUBUQUE COUNTY, White Pine Hollow State Forest Reserve, *R. F. Thorne 30115* (IA); EMMET COUNTY, High Lakewoods, *B. O. Wolden 886* (ISC); FAYETTE COUNTY, 4 mi. NE of West Union, "Dutton's Cave," *M. Murley 272* (ISC); FRANKLIN COUNTY, 6 mi. S of Hampton, *P. H. Monson 3637* (ISC); FREMONT COUNTY, Sidney, *L. Pammel 402* (GH, ISC); GRUNDY COUNTY, 3.5 mi. W of Grundy Center, *L. J. Eilers 4036* (IA); GUTHRIE COUNTY, 5 mi. NE of Guthrie Center, *P. H. Monson 3327* (ISC); HAMILTON COUNTY, 2 mi. S of Webster City, *P. H. Monson 852* (ISC); HANCOCK COUNTY, edge of acid bog, *R. D. Albertson 171-60* (ISC); HARDIN COUNTY, 4 mi. E of Hubbard, *P. H. Monson 2747* (ISC); HENRY COUNTY, Mt. Pleasant, *J. H. Mills 712* (IA); HOWARD COUNTY, Turkey R. area, *L. J. Eilers 2151* (IA); HUMBOLT COUNTY, N side of Hwy 222 at W edge of Livermore, *P. H. Monson 3544* (ISC); IOWA COUNTY, N of Middle Amana, *W. Easterly 548* (ARIZ, IA, MT); JACKSON COUNTY, Bellevue State Park, *T. S. Cooperrider 2042* (MIN); JASPER COUNTY, Rock Creek Township, Victor Grange, *T. van Brugger 602* (DAO); JEFFERSON COUNTY, Center Township, behind Golf Course, *C. L. Gilly & M. McDonald 917* (ISC); JOHNSON COUNTY, Newport, *D. Corwin 55* (IDS); JONES COUNTY, Hale Township, Sec. 24, NW¼, *T. S. Cooperrider 1854* (MIN, NCU); LEE COUNTY, Sec. 29, SE¼, T66N, R6W, *R. Davidson 2289* (IA, US); LINN COUNTY, Cedar Rapids, *G. H. Berry in 1913* (IA); LOUISA COUNTY, Muscatine Island, *P. C. Myers in 1897* (IA); MADISON COUNTY, SW of Winterset Backbone, *B. Shimek in 1919* (ISC); MAHASKA COUNTY, bluffs 14 mi. SW of Oskaloosa, *D. W. Augustine 333a* (ISC, OKL); MARION COUNTY, Summit Township, Sec. 29, *T. van Brugger 2472* (ASU); MITCHELL COUNTY, S of St. Ansgar along the Cedar River, *B. Shimek in 1930* (ISC); MONONA COUNTY, Preparation Canyon State Park, *J. L. Carter 3173* (IA); MUSCATINE COUNTY, 8 mi. NW of Muscatine, *B. Shimek in 1925* (MIN); PAGE COUNTY, 5 mi. SW of Clarinda, *M. J. Fay 5729* (IA); POLK COUNTY, Margo Frankell State Park, *T. van Brugger 2388* (IA, SMU); POWESHIEK COUNTY, Warren Township, Sec. 5, *M. J. Huston 51* (GRI); STORY COUNTY, Ames, *L. H. Pammel & C. R. Ball 24* (GH, ISC, MO, NY, US); TAMA COUNTY, Gladbrook, *L. H. Pammel in 1929* (ISC); TAYLOR COUNTY, Lake of Three Fires State Park, *M. J. Fay 3966* (IA, UC); UNION COUNTY, Creston, *T. L. Andrews in 1880–1882* (ISC); VAN BUREN COUNTY, 1¼ mi. NNW of Hillsboro, *R. A. Davidson 356* (IA, NCU, SMU); WARREN COUNTY, Lake Ahquabi State Park, *T. van Brugger 980* (IA); WASHINGTON COUNTY, 1 mi. N of Kalona, English River Township, *B. L. Wagenknecht 591* (IA); WEBSTER COUNTY, Otho Township, Woodman's Hollow State Park, *M. Lelong M128* (ISC); WINNEBAGO COUNTY, Forest City Park, *P. H. Monson 3713* (ISC); WINNESHIEK COUNTY, Calmar, *W. L. Tolstead in 1933* (MO); WORTH

COUNTY, Hanlantown, *L. H. Pammel in 1902* (ISC); WRIGHT COUNTY, Rowan, *K. Whited 2733* (OSC). KANSAS: ATCHISON COUNTY, 4 mi. N, 2 mi. W of Atchison, *S. Stephens 57926* (KANU); BOURBON COUNTY, Devon, on Berlin Hill, *Z. Thompson 674* (KANU); CHEROKEE COUNTY, no further data, *G. L. Clothier & H. N. Whitford in 1897* (KSC); COFFEY COUNTY, 5.2 mi. N of Aliceville, *L. Magrath 6166* (KANU); DONIPHAN COUNTY, 0.7 mi. SE of the Kansas-Nebraska line on K7, *L. Magrath 5906* (KANU); DOUGLAS COUNTY, 1.5 mi. E and 2 mi. S of Baldwin City, *J. E. Bare 2350* (KANU, MASS, VDB); FRANKLIN COUNTY, 1 mi. E, 3 mi. S of Homewood, *S. Stephens & R. Brooks 32717* (ASU, KANU, NLU, VDB); GREENWOOD COUNTY, Eureka, *A. S. Hitchcock in 1892* (KSC); JEFFERSON COUNTY, N of New Perry, *J. E. Bare 2541a* (KANU, NY); JOHNSON COUNTY, Olathe, *A. S. Hitchcock in 1892* (KSC); LEAVENWORTH COUNTY, 3 mi. W, 1.5 mi. N of Tonganoxie, *S. Stephens 58888* (KANU); LINN COUNTY, 2 mi. N of Trading Post, *R. McGregor 10498* (KANU); LYON COUNTY, 1 mi. N and 1 mi. W of Reading, *J. Wilson 9100* (?); MARSHALL COUNTY, no further data, *G. L. Clothier & H. N. Whitford in 1897* (KSC); MIAMI COUNTY, no further data, *G. L. Clothier & H. N. Whitford in 1897* (KSC); NEMAHA COUNTY, no further data, *A. S. Hitchcock in 1896* (KSC); NEOSHO COUNTY, 6 mi. E of Chanute along Big Creek, *W. W. Holland 145* (KSC); POTTAWATOMIE COUNTY, Pottawatomie State Lake no. 1, *W. Barker 4256* (GH, KANU, UARK); RILEY COUNTY, woods, *J. B. S. Norton 690* (GH, KSC, MO, NMU, NY, RM, US); SHAWNEE COUNTY, 1 mi. S of Elmont, *L. Volle 321* (KANU); WOODSON COUNTY, Grassland, creek banks, *W. Harr in 1930* (KANU); WYANDOTTE COUNTY, 1 mi. S, 1 mi. E of Piper, *G. Seiler & R. Brooks 5346* (KANU). KENTUCKY: ANDERSON COUNTY, Wildcat Road, *M. E. Wharton 10062* (KY); BARREN COUNTY, 3 mi. SW of Glasgow, *H. A. Gleason 8857* (NY); BATH COUNTY, Olympian Springs, *M. E. Wharton 2539a* (KY, MICH, MO); BELL COUNTY, Pine Mt. State Park, Bear Wallow Gap, *E. J. Carr in 1965* (KY); BOYLE COUNTY, 0.75 mi. W of Junction City, *M. E. Wharton 2961* (MICH); BREATHITT COUNTY, Robinson Forest, *D. M. Smith 1634* (KY, NCU); BULLITT COUNTY, Bernheim Forest, *C. R. Gunn 92* (NCU); CALDWELL COUNTY, Pennyrite State Park, *G. E. Hunter & D. F. Austin 1723* (MUR, NCU); CALLOWAY COUNTY, 2 mi. N of junction hwy 121 & 1386 on 1386, W Fork Clarks R., *V. A. Funk 667* (MO); CARLISLE COUNTY, near junction of Laketon Road and railroad tracks, *G. E. Hunter & J. L. Gentry 3220* (MUR); CASEY COUNTY, 9 mi. N of Liberty, *M. E. Wharton 4721* (KY, MO, NY); CLARK COUNTY, near Oil Springs, *M. E. Wharton 4614* (DHL, KY, MICH, NY); CRITTENDEN COUNTY, 1¼ mi. SE of Crayne, *G. E. Hunter & D. F. Austin 1943* (MUR, NCU); EDMONSON COUNTY, Mammoth Cave National Park, Doyle Valley, *B. B. McInteer 569* (WIS); ESTILL COUNTY, 2.5 mi. SE of Red River on Winchester-Irvine Road, *M. E. Wharton 2997* (KY, WIS); FAYETTE COUNTY, Boone Creek near the Kentucky River, *M. E. Wharton 9034* (DHL); FLEMING COUNTY, 4 mi. SE of Plummer's Mill, *M. E. Wharton 4513* (MICH, TENN); FRANKLIN COUNTY, near Rocky Branch, *M. E. Wharton 10938* (KY); FULTON COUNTY, near U.S. 45, SW of Fulton, *B. B. McInteer 1760* (KY); GARRARD COUNTY, White Oak Creek, *M. E. Wharton 10099* (KY); GRANT COUNTY, 1.6 mi. from junction of Fort Mill Road and Ky. 36, *E. M. & E. T. Browne, Jr. 4634* (MEM); GRAVES COUNTY, 2 mi. SE of Mayfield Woods, *D. O'Dell & D. Windler 871* (SIU); GRAYSON COUNTY, U.S. 62, 8 mi. E of junction of U.S. 62 & Ky. 105 in Caneyville, *E. M. & E. T. Browne, Jr. 7541* (KY, MEM); GREENUP COUNTY, 3 mi. from Boyd County line, "Big Woods," *L. Smith et al. 3579* (US); HARLAN COUNTY, Big Black Mt., *T. H. Kearney, Jr. 212* (CAN, ISC, MIN, NY, OS, US); HENDERSON COUNTY, Audubon Park, *G. E. Hunter & D. F. Austin 2284* (MUR, NCU); HENRY COUNTY, 0.6 mi. N of Union Church, 2 mi. N of U.S. 421, *J. L. Gentry, Jr. 408* (KY, MEM, NCU, NY); HOPKINS COUNTY, Ky. 70, 2.8 mi. E of junction of Ky. 70 & Ky. 109 at Beulah, *E. M. & E. T. Browne, Jr. 7737* (KY, MEM, NCU); JEFFERSON COUNTY, Goose Creek, *Davies in 1944* (DHL); JOHNSON COUNTY, Little Mine Fork of Paint Creek, 1 mi. N of Hargis, *D. Keil & M. Roberts 3947* (OS); LETCHER COUNTY, near U.S. 119 on N side of Pine Mt., *B. B. McInteer 1912* (KY); LEWIS COUNTY, 2 mi. SW of Petersville, *M. E. Wharton 5459* (KY); LIVINGSTON COUNTY, Hwy 133 N to bridge crossing Deer Creek, *R. Athey 232* (MEM); LYON COUNTY, Kentucky Woodlands National Wildlife Refuge, *R. L. Buck 204* (BHO); MADISON COUNTY, Cowbell Lake, *J. Grossman 128* (KY, LL); MARION COUNTY, 2.75 mi. SE of New Market, *M. E. Wharton 4665* (MICH, NCSC, NY); MARSHALL COUNTY, 0.6 mi. from Calloway County line on rte 94E, *R. Athey 1851* (MEM); MCCRACKEN COUNTY, Riedland Community, *R. Athey 668* (MEM); MCCREARY COUNTY, Daniel Boone National Forest, Great Meadows Campground, *E. M. & E. T. Browne, Jr. 72E8,6* (MEM); MCLEAN COUNTY, Bates Knob near Semway, *J. Conrad 1671* (KY); MENIFEE COUNTY, Skidmore Creek, *H. L. Setser 614* (KY); MERCER COUNTY, near Oregon, *M. E. Wharton 10198* (KY); MONTGOMERY COUNTY, 1.75 mi. SE of Jeffersonville, *M. E. Wharton 2844* (MICH); OLDHAM COUNTY, Shiloh Lane at Harrods Creek, *J. J. Mathews 371* (DHL); POWELL COUNTY, near Nada Tunnel, *P. D. Higgins 1562* (DHL); ROCKCASTLE COUNTY, near Copper Creek, *M. E. Wharton 2636* (MICH, NCSC, TENN); ROWAN COUNTY, S of Triplett, *M. E. Wharton 6501* (DHL, KY); SIMPSON COUNTY, Robey's Swamp near Franklin, *G. E. Hunter et al. 2830* (MUR, NCU); TRIGG COUNTY, 0.25 mi. SE of marker 7E4, *W. H. Ellis 01365* (ISC, NLU, TENN); UNION COUNTY, near McCotrey school, *H. Shacklette 382* (NY); WARREN COUNTY, 3 km N of Hadley, Clifty

Hollow, *J. Conrad 230* (MO). LOUISIANA: BIENVILLE PARISH, SE of Bryceland, 1 mi. E of La. 9, *R. D. Thomas et al. 49449* (DUR, NLU, UARK); EAST FELICIANA PARISH, Jackson, *W. M. Carpenter (1811–1848)* (NO); WEST FELICIANA PARISH, Alexander's Creek N of hwy 35, *C. Brown 7235* (LSU), ca. 15 mi. N of St. Rosemound, *Curry et al. 524* (LSU), between Tunica & Turnbull, gorges N of La. 66, *R. D. Thomas 49261* (NLU). MAINE: ANDROSCOGGIN COUNTY, South Poland, *K. Furbish in 1897* (NEBC); AROOSTOOK COUNTY, Mt. Horse, *G. R. Cooley & A. S. Pease 6848* (NCU); CUMBERLAND COUNTY, Cumberland, *E. Chamberlain in 1901* (NEBC); FRANKLIN COUNTY, Farmington, Sandy R. near rte 4 & village of Fairbanks, *G. B. Rossbach 6383* (ACAD, NCU, WVW); HANCOCK COUNTY, Orland, *H. Atkins* (NEBC); KENNEBEC COUNTY, Gardiner and vicinity, *N. C. Fassett in 1935* (WIS); KNOX COUNTY, above SW shore of Megunticook Lake, rte 105, Camden, *G. B. Rossbach 6680* (WVW); OXFORD COUNTY, Paris, near Snow's Falls, *A. Norton 19130* (NEBC), Gilead, *A. S. Pease 17428* (NEBC), Canton, *J. Parlin 2059* (GH, NEBC); PENOBSCOT COUNTY, Orono, Sutton woodlot, *E. C. & E. B. Ogden 2370* (DAO, OKL, TEX, US), South Dixmont, summit of Mt. Harris, *G. Rossbach 223?* (ACAD); SAGADAHOC COUNTY, ski area in Topsham, *R. M. Downs 4705* (NCSC); SOMERSET COUNTY, Skowhegan, *R. C. Bean in 1934* (NEBC), Moscow, Austin Stream, *J. Collins & E. Chamberlain in 1902* (NEBC); WALDO COUNTY, Freedom, Beaver Ridge, *G. B. Rossbach 1810* (ACAD, WVW); YORK COUNTY, South Berwick, The Gorge, *O. M. Neal, Jr. in 1935* (MIN). MARYLAND: ALLEGHENY COUNTY, ca. 1 mi. SE of Westernport, *R. M. Downs 6980* (NCU); ANNE ARUNDEL COUNTY, 0.25 mi. N of Priests Bridge, near Bowie, *E. H. Walker & F. R. Fosberg 2846* (GA); BALTIMORE COUNTY, woods, 2103 Bluemont Road, *W. E. Brumback 76-22* (BALT); CALVERT COUNTY, Scientist's Cliffs, Parker Creek, *F. C. Seymour 17288* (MO); CARROLL COUNTY, 3 mi. N of Eldersburg on rte 32, *T. D. Misotti 76-004* (BALT); CECIL COUNTY, E of North East, *F. Hermann 3411* (NA); FREDERICK COUNTY, Catoctin Mt. Park, *C. J. Hickey II 64* (BALT, NCU); GARRETT COUNTY, Bubbling Spring, Washington Camp, *J. A. Nieuwland in 1933* (ND); HARFORD COUNTY, Rocks, Deer Creek State Park, *D. L. Windler & Keenan 3117* (BALT, BRY, FSU, GAS, H, KANU, LTU, MASS, NCU, OSC, PAC, SIU, TENN, VSC, WILLI); HOWARD COUNTY, Grace Chemical Co. woods, rte 32, *J. Engh in 1964* (MARY); KENT COUNTY, Lloyd's Creek Spit, *P. Gladu in 1965* (MARY); MONTGOMERY COUNTY, 3 mi. ESE of Rockville, *F. R. Fosberg 19012* (NA); PRINCE GEORGES COUNTY, Suitland, *C. P. Smith 3193* (DS); QUEEN ANNES COUNTY, near Chestertown, *E. Vanatte in 1904* (PH); TALBOT COUNTY, Arcadia, near Easton, *F. Shreve in 1902* (ARIZ); WASHINGTON COUNTY, Round Top, ca. 3 mi. SW of Hancock, *R. M. Downs 1131* (NCU). MASSACHUSETTS: BARNSTABLE COUNTY, Spring Hill, Sandwich, *M. L. Fernald & B. Long 18851* (NEBC, PH); BERKSHIRE COUNTY, Beckett, *G. N. & F. F. Jones 17214* (CM, IA, MIN, MO, NY), Lanesboro, *J. R. Churchill in 1915* (MO); BRISTOL COUNTY, Easton, *C. Blomberg in 1901* (NEBC); DUKES COUNTY, Martha's Vineyard, Menemsha, Chilmark, *F. C. Seymour 10035* (DAO, DUKE, SMU); ESSEX COUNTY, Boxford, *L. E. Richardson in 1962* (MO); FRANKLIN COUNTY, Colrain, *A. S. Goodale 61131* (OKL); HAMPDEN COUNTY, Wilbraham, Mt. Wilbraham, *F. C. Seymour 684* (DUKE, MO, NY, SMU, WIS); HAMPSHIRE COUNTY, Hatfield, Horse Mountain, *H. E. Ahles 77723* (ASU, BALT, CM, DS, GA, H, ISC, KANU, KYO, MA, MASS, MEM, MIN, MISS, NDA, NHA, NLU, OKLA, PAC, SMU, TENN, UBC, UMO, VPI, WTU, WVA); MIDDLESEX COUNTY, Winchester, *E. Rouleau, L. B. & C. B. Smith, Pl. Exsic. Grayanae 1374* (B, BH, CAN, CAS, COLO, CU, DAO, DS, DUKE, GA, GH, IA, ILL, IND, ISC, KANU, KY, LL, LTU, MASS, MICH, MIN, MO, MT, NA, NCU, NHA, NO, NY, NYS, OKL, OKLA, OSC, PAC, PENN, PH, POM, RM, SMU, TENN, TEX, TNS, TRT, UARK, UBC, UC, US, UTC, WIS, WS, WVA); NANTUCKET COUNTY, Wawwinet, *E. Prediger in 1969* (VDB); NORFOLK COUNTY, Stoughton, *S. F. Blake 6488* (LL); PLYMOUTH COUNTY, Duxbury Beach, *H. St. John 789* (NEBC); SUFFOLK COUNTY, Oak Island, *R. A. Ware in 1906* (VDB); WORCESTER COUNTY, W of Camp Putnam, *P. H. Raven & O. Solbrig 16505* (KYO, MHA, MO); Lunenburg, *B. N. Gates 26233* (NEBC). MICHIGAN: ALCONA COUNTY, ca. 1 mi. S of Curran, *E. G. Voss 4675* (MICH); ALLEGAN COUNTY, W shore of Green Lake, *C. W. Bazuin 3047* (MICH); ARENAC COUNTY, ca. 8.5 mi. N of Standish, *E. G. Voss 4644* (MICH); BAROGA COUNTY, Ford Forestry Center, *E. A. Bourdo, Jr. 28602* (H, NLU, W); BENZIE COUNTY, N side of Crystal Lake, *F. C. Gates 20835* (KSC); BERRIEN COUNTY, Warren Woods, *C. Billington in 1919* (MICH); BRANCH COUNTY, Bronson, *C. A. Brown 2572* (WIS); CASS COUNTY, ca. 5 mi. SW of Edwardsburg, *E. G. Voss 7534* (MICH); CHARLEVOIX COUNTY, ca. 9 mi. E of Boyne Falls, *E. G. Voss 13487* (MICH); CHEBOYGAN COUNTY, Vincent Lake, *F. C. & M. T. Gates 10670* (MO); CLINTON COUNTY, Essex Township, Sec. 10, T8N, R3W, *G. W. Parmelee 2726* (TEX, VDB); DELTA COUNTY, Burnt Bluff, *F. Hermann 6315* (MICH, NA, POM); EATON COUNTY, Hamlin Township, Sec. 12, T1N, R3W, *G. W. Parmelee 2753* (TEX); EMMET COUNTY, Wycamp River woods, *F. C. Gates 22241* (KSC, OKL, OKLA, UMO, WIS); GENESEE COUNTY, Flint, Glenwood Cemetery, *E. E. Sherff in 1907* (POM); GRAND TRAVERSE COUNTY, ca. 6 mi. SE of Traverse City, *J. V. A. Dieterle 1854* (CM, MICH); GRATIOT COUNTY, about Alma, *C. A. Davis in 1892* (WS); HILLSDALE COUNTY, 7 mi. SE of Hillsdale, *E. G. Voss 7453* (MICH); HOUGHTON COUNTY, E of Chassell, bank of Sturgeon, *R. C. Richards 1288* (ACAD, IDS); INGHAM COUNTY, Michigan

State Univ. campus, Baker Woodlot, *W. D. Stevens 1617* (KYO); JACKSON COUNTY, Waterloo Township, Sec. 15, T1S, R2E, *G. W. Parmelee 673* (FSU); KALAMAZOO COUNTY, Kellogg Forest, *MSU Botany 203-S Class 47* (OKL); KENT COUNTY, Courtland Township, Sec. 24, T9N, R10W, *G. W. Parmelee 1292* (VDB); LAPEER COUNTY, ca. 6 mi. SW of Metamora, *E. G. Voss 7291* (MICH); LIVINGSTON COUNTY, Greenoak Township, Island Lake State Recreation Area, *D. Lynch in 1947* (SMU); MACKINAC COUNTY, St. Ignace, 1.5 mi. N of hwy U.S. 2, *H. H. Bartlett & C. D. Richards 362* (DAO, MT, TRT); MANISTEE COUNTY, ca. 7.5 mi. E of Brethren, *E. G. Voss 11148* (MICH); MASON COUNTY, Riverton Township, ca. 3.5 mi. SW of Scottville, *E. G. Voss 11179* (MICH, TRT); MECOSTA COUNTY, ca. 2 mi. W of Big Rapids, *E. G. Voss 7598* (MICH); MENOMINEE COUNTY, Kinepoway Red Oak Stand no. 25, *G. Goff in 1964* (NCU); MONROE COUNTY, 4.5 mi. S of Milan, *B. Robertson 319* (MICH); MONTCALM COUNTY, ca. 6 mi. SW of Sheridan, *E. G. Voss 7588* (MICH); MONTMORENCY COUNTY, 3.5 mi. S of hwy 32, *R. Perdue 7104* (NA); MUSKEGON COUNTY, Dalton Township, *E. A. Bourdo, Jr. 121* (MICH); NEWAYGO COUNTY, shore of Kimball Lake, *C. W. Bazuin 3511* (MICH); OAKLAND COUNTY, Parkedale, *O. A. Farwell in 1914* (MICH, WIS); OCEANA COUNTY, Pentwater, *Miller in 1928* (GA); OSCEOLA COUNTY, 4 mi. WSW of Tustin, *E. G. Voss 14220* (MICH); ST. CLAIR COUNTY, Port Huron, *C. K. Dodge in 1896* (NCU, TENN); ST. JOSEPH COUNTY, Lockport Township, Sec. 34, T6S, R11W, *G. W. Parmelee 17211* (FSU, TEX); SANILAC COUNTY, near Shabonna, *E. G. Voss 7351* (MICH); SHIAWASSEE COUNTY, Owosso, *G. H. Hicks in 1889* (MIN); TUSCOLA COUNTY, ca. 1 mi. NW of Mayville, *E. G. Voss 7350* (MICH); VAN BUREN COUNTY, 3–4 mi. N of Paw Paw, *E. Shear, Jr. in 1921* (CU); WASHTENAW COUNTY, 0.75 mi. W of Scio, *F. J. Hermann 6280* (MICH, MIN, MO, NA, PH, POM, WIS); WAYNE COUNTY, Flat Rock, *O. Farwell 7450* (GH); WEXFORD COUNTY, ca. 8 mi. NW of Cadillac, *E. G. Voss 3284* (MICH). MINNESOTA: ANOKA COUNTY, Carlos Avery Refuge, *R. J. Benson 93* (MIN); BECKER COUNTY, Detroit Lakes, *O. Stevens in 1933* (OSC); BELTRAMI COUNTY, 4 mi. NW of Panemah, *J. W. Moore & N. L. Huff 19161* (DAO, MIN); BENTON COUNTY, 2 mi. SW of Foley, *J. W. Moore & N. L. Huff 18863* (MIN, RM, WVA); BLUE EARTH COUNTY, 3 mi. W of Mankato, *J. W. Moore 26764* (IA, MIN); BROWN COUNTY, Sleepy Eye, *E. P. Sheldon S1038* (MIN); CARVER COUNTY, Page Lake, *C. A. Ballard B757* (MIN); CASS COUNTY, Gulf Lake, Sandy Point, *A. Chandler 1559* (MO); CHISAGO COUNTY, Center City, *J. Sandberg 661* (ISC, US); CLAY COUNTY, Buffalo State Park, *O. A. Stevens in 1962* (NDA), 5 mi. S of Moorehead, Forest Stand no. 12, *W. J. Wanek 311* (NDA), along the Wild Rice River at Ulen, *J. W. Moore 23663* (MIN); CLEARWATER COUNTY, Itasca Park, Bear Point, *J. B. Moyle 940* (CU, DUL, MO, NY, POM, SMU, UC); CROW WING COUNTY, Garrison Township, E of Chandler Lake, *J. W. & M. F. Moore 261* (MIN); DOUGLAS COUNTY, 1 mi. NW of Evansville, *J. W. Moore 21320* (MIN, NDA); FARIBAULT COUNTY, Sec. 7, SW¼ of the SE¼, T101N, R27W, *T. Morley 970* (MIN); GOODHUE COUNTY, along the Zumbro R., *W. L. Tolstead in 1933* (COLO); HENNEPIN COUNTY, Lake Minnetonka, N shore Brown's Bay, *H. A. Hedman 34* (MIN); HOUSTON COUNTY, Crooked Creek, *W. A. Wheeler 270* (MIN); ITASCA COUNTY, Bowstring, *H. E. Stork in 1925* (GRI), ca. 30 mi. NW of Grand Rapids, *G. A. Wheeler & P. N. Glaser 1857* (DUR, NCU); KANABEC COUNTY, NE shore of Knife Lake, *J. W. Moore & D. L. Jacobs 14971* (ISC, MIN); KANDIYOHI COUNTY, Willmar, *W. D. Frost in 1892* (CU, ISC, MIN, OKL, UC, UTC, WIS); LAKE COUNTY, Manomin Lake portage, *C. Ahlgren 2822* (DUL, TRT), Rice Bay area of Basswood Island, *O. Lakela et al. 18066* (TRT); LAKE OF THE WOODS COUNTY, vicinity of Fort St. Charles, Magnuson Island, *J. W. & M. F. Moore 11270* (MIN, TRT, US), Lake of the Woods, Four Mile Bay, *J. W. & M. F. Moore 12208* (BRY, MIN, SMU); MEEKER COUNTY, near Dassel, old Trousdail Farm, *H. L. Dale in 1925* (DS); MILLE LACS COUNTY, Milaca, *E. P. Sheldon in 1892* (MIN, ORE, RM, US, WIS, WS); MORRISON COUNTY, Center Valley, *J. W. Moore & N. L. Huff 18001* (DAO, MIN, NDA); NICOLLET COUNTY, Courtland, *C. A. Ballard B1022* (MIN); NORMAN COUNTY, 3 mi. E, 1.3 mi. N of Syre, *G. B. Ownbey & F. Ownbey 2279* (KE, MIN); OTTER TAIL COUNTY, Lake Lida, *E. P. Sheldon S3769* (MIN); PINE COUNTY, near the NE corner of St. Croix State Park, *J. W. Moore & N. L. Huff 18102* (MIN); POLK COUNTY, 4 mi. S of Bygland, Forest Stand no. 30, *W. J. Wanek 447* (NDA); POPE COUNTY, Glenwood, *B. C. Taylor T886* (MIN); RAMSEY COUNTY, St. Paul, *T. S. Roberts in 1884* (MIN); RED LAKE COUNTY, woods of Clearwater R., *O. A. Stevens & D. R. Moir in 1960* (NDA); REDWOOD COUNTY, Redwood Falls, *E. P. Sheldon S940* (MIN); RICE COUNTY, Nerstrand Woods, *Linnaean Club, U. of Minn. 270* (MIN); ST. LOUIS COUNTY, Duluth, along Fischer Creek, Hunter's Hill, *O. Lakela 4736* (DUL, ISC, MIN, SMU, WIS, WS), Prairie Lake, SW corner of the county, *O. Lakela 7881* (DUL, MIN), Lake Kabetogoma, near Point Park Resort, *O. Lakela 9479* (DAO, DUL, MIN), Eureka, *H. Eggert in 1887* (RM); SCOTT COUNTY, Prior's Lake, *C. A. Ballard B493* (MIN); STEARNS COUNTY, Collegeville, *P. E. Kuehne in 1933* (DAO), St. Joseph, SBC woods, *Sister R. Westkaemper in 1966* (MIN); TRAVERSE COUNTY, Sec. 31, T126N, R48W, *R. P. Williams 2352* (NDA); WABASHA COUNTY, Lake City, (MIN *159745*); WASECA COUNTY, E shore of Lake Elysian, *J. W. Moore & Y. T. Hsi 23473* (MIN); WINONA COUNTY, Winona, *G. W. Freiberg in 1912* (MO); WRIGHT COUNTY, 1 mi. NW of Annandale, *J. W. Moore & D. L. Jacobs 14619* (MIN). MISSISSIPPI: ADAMS COUNTY, 1.8 mi. S of junction U.S. hwys 61-84 at Natchez, *L. C. Temple 11225* (MISS); DESOTO COUNTY, ca. 1 mi. ESE of Walls, *S. McDaniel 11667* (GA, MO, VDB); LAFAYETTE

COUNTY, Taylor, *L. Boil in 1914* (MISS); PANOLA COUNTY, 6 mi. W of Batesville, Tallahatchie R., *J. D. Ray 6887* (CAS, GA, OKLA); TATE COUNTY, W end of Arkabutla Dam, *T. M. Pullen 66354* (MISS); WARREN COUNTY, 8 mi. N of Bovina, *T. H. Pullen 64606, 64612* (MISS); WILKINSON COUNTY, ca. 9 mi. W of Woodville, *K. Rogers 8402* (NCU, TENN, VDB). MISSOURI: ANDREW COUNTY, 3.5–4 mi. SE of Fillmore, *J. A. Steyermark 70002* (UARK); BARRY COUNTY, Eagle Rock, *B. Bush 38* (MO, US); BARTON COUNTY, 3 mi. NE of Milford, *E. J. Palmer 52893* (UMO); BOLLINGER COUNTY, 5 mi. W of Grassy, *J. A. Steyermark 14149* (MO); BOONE COUNTY, woods on prairie N of Columbia, *H. W. Rickett in 1929* (UMO); CAPE GIRARDEAU COUNTY, near Cape Girardeau, *E. J. Palmer 18009* (MO); CEDAR COUNTY, Bear Creek, *W. Trelease 341* (MO); CHRISTIAN COUNTY, 4 mi. SE of Chadwick, *J. A. Steyermark 23053* (MO); CLAY COUNTY, no further data, *B. F. Bush 12754* (MO, UMO, WIS); CLINTON COUNTY, ca. 6 mi. S of Cameron, *J. A. Steyermark 14917* (MO); DENT COUNTY, Montauk State Park, *R. D. Thomas et al. 9694* (NLU); DOUGLAS COUNTY, beside White R. and Mo. 14 at Twin Bridges, *R. D. Thomas et al. 15760* (NLU); FRANKLIN COUNTY, Meramec State Park, *J. M. Mason in 1938* (UMO); GREENE COUNTY, vicinity of Springfield, *P. C. Standley in 1905* (US); HARRISON COUNTY, 5–6 mi. N of Cainsville, *J. A. Steyermark 40313* (MO); HICKORY COUNTY, E of Jordan, along Little Niangua R., *J. A. Steyermark 13349* (MO, UMO); IRON COUNTY, Iron Mt., Lake, *J. H. Kellogg 1895* (MO); JACKSON COUNTY, Courtney, *B. F. Bush 7690* (GH, MIN, NY); JASPER COUNTY, Webb City, Lakeside Park, *E. J. Palmer 469* (MIN, MO); JEFFERSON COUNTY, 1 mi. N of Pevely on Marble Springs Road, *G. Davidse 3427* (MO); JOHNSON COUNTY, near Columbus, *E. J. Palmer 36726* (MO); LAWRENCE COUNTY, 3 mi. NE of Lawrenceburg, *E. J. Palmer 52380* (SIU, MO); LEWIS COUNTY, 0.5 mi. S of Monticello, *J. A. Steyermark 25649* (MO); LINCOLN COUNTY, Cuivre River State Park, *W. T. Kennell in 1970* (MO); LIVINGSTON COUNTY, NW of Chillicothe, *S. Sparling 997* (ISC); MARIES COUNTY, ca. 4 mi. E of Shantytown, *P. L. Redfearn 21668* (NCU); MARION COUNTY, Hannibal, Riverview Park, *J. Davis 9024* (DAO); MILLER COUNTY, between Sudheimes & Iberia, *J. A. Steyermark 13035* (MO); MORGAN COUNTY, Osage R. near mouth of Proctor Creek, *J. A. Steyermark 13164* (MO); NEWTON COUNTY, 3.5 mi. NW of Wentworth, near Haddock Spring, *E. J. Palmer 58002* (UMO); NODAWAY COUNTY, W of Clearmont, Nodaway R., *J. A. Steyermark 5877* (MO); OREGON COUNTY, ca. 3 mi. NW of New Liberty, *P. L. Redfearn 12734* (FSU, UMO, VDB); OZARK COUNTY, NE of Tecumseh, Althaea Springs, *R. D. Thomas et al. 31224* (NLU, TENN); PERRY COUNTY, 3 mi. N of Menfro, *J. A. Steyermark 14036* (MO); PHELPS COUNTY, Jerome, *J. H. Kellogg 122* (MO); PLATTE COUNTY, Farley, *B. F. Bush 11799* (MIN, MO, NY, SMU, UMO); POLK COUNTY, 0.5 mi. N of Burns, *J. A. Steyermark 13573* (MO, UMO); RALLS COUNTY, near New London, bluffs of Salt R., *E. J. Palmer & J. A. Steyermark 40719* (MO); REYNOLDS COUNTY, ca. 10 mi. SE of Redford, *J. A. Steyermark 14223* (MO); ST. GENEVIEVE COUNTY, Terre Bleue Creek, *W. Trelease 1039* (MO); ST. LOUIS CITY, *N. Riehl 116* (MO); ST. LOUIS COUNTY, Creve Couer Lake, *J. H. Kellogg in 1927* (MO); SALINE COUNTY, 5 mi. SW of Miami, Van Meter State Park, *J. A. Steyermark 20432* (MO); SHANNON COUNTY, vicinity of Jam-up Cave, *P. L. Redfearn et al. 824* (MO, NCU); STONE COUNTY, 1 mi. NW of Marmaros, *J. A. Steyermark 22619* (MO); TANEY COUNTY, 1.5–2 mi. N of Mincy, *J. A. Steyermark 5542* (MO); WARREN COUNTY, tributary to Lost Creek, *C. O. Marvin 422* (MO); WAYNE COUNTY, Williamsville, *C. T. in 1900* (UMO). NEBRASKA: BROWN COUNTY, Long Pine, *J. M. Bates in 1911* (MIN); CASS COUNTY, Wabash, *T. Williams in 1889* (US); CHERRY COUNTY, NE of Valentine at Niobrara National Wildlife Refuge, *S. P. Churchill 4494* (MO, NDA, NEB, NLU, NY); DODGE COUNTY, near Fremont, *C. Engberg in 1894* (NEB); DOUGLAS COUNTY, campus of Univ. of Nebraska at Omaha, *D. Sutherland 1865* (OMA); FRANKLIN COUNTY, streams and hillsides, *Hussong 4697* (NEB); HALL COUNTY, along Platte River S of Grand Island, *R. Lemaire* 2558 (NEB); HOOKER COUNTY, near the Forks of Dismal R., *P. A. Rydberg 1463* (GH, NY); NEMAHA COUNTY, Peru, *J. Winter 41* (US); OTOE COUNTY, Nebraska City, *J. Winter 76* (US); RICHARDSON COUNTY, Sec. 26, T1N, R18E, Rulo-White Cloud Road, *P. Shildneck C-6701* (NEB); SARPY COUNTY, near Gretna Fish Hatchery, *S. P. Churchill 6097* (KANU, MO, NDA, NEB, NLU); SHERIDEN COUNTY, Pishelville, *F. Clements 2766* (BH, GH, MIN, NEB, US); THOMAS COUNTY, near Plummer Ford, Dismal R., *P. A. Rydberg 1463* (H, NEB, NY, US); THURSTON COUNTY, 1.5 mi. E of hwy junction 73-94, Sec. 13, T25N, R9E, *S. P. Churchill 7912* (KANU, MO, NDA, NEB, NLU); WASHINGTON COUNTY, Neale Woods, *M. W. Antrim 56* (OMA). NEW HAMPSHIRE: CARROLL COUNTY, town of Wonalancet, Cold R., *L. K. Henry in 1971* (CM); CHESHIRE COUNTY, town of Surry, *D. E. Boufford 18860* (BM, CM, E, KYO, LD, MHA, MO, PE); COOS COUNTY, Shelburne, under cliffs of Crag, *W. Deane in 1917* (CU, MIN, SMU, TEX); GRAFTON COUNTY, Hanover, *H. Barss in 1910* (OSC); HILLSBOROUGH COUNTY, Wilton, *B. B. Lambert 13* (WS); MERRIMACK COUNTY, Hill, Murray Hill, *C. Bullard in 1932* (NEBC); ROCKINGHAM COUNTY, Derry, *C. F. Batchelder in 1913* (NEBC); STRAFFORD COUNTY, Madbury, Laton Farm, *A. R. Hodgdon 12977* (DAO, NHA); SULLIVAN COUNTY, Unity, *F. C. Seymour 20890* (MO, SMU). NEW JERSEY: BERGEN COUNTY, Fort Lee, *E. Magee in 1901* (GH); BURLINGTON COUNTY, Arneytown, *R. R. Driesbach 1545* (CM); CAMDEN COUNTY, NE of Haddonfield, *J. Fogg 7639* (CU, PH); CUMBERLAND COUNTY, Roadstown, Chestnut Run, *B. Long 41341* (PH); ESSEX COUNTY, Caldwell, *L. H. Lighthipe in 1917* (MO); GLOUCESTER COUNTY, Black-

wood, S Branch Turkey Creek, *B. Long 16847* (DS); HUNTERDON COUNTY, Kingwood Township, Wickecheoke Creek at Locktown, *M. L. Roberts 2491* (OS); MERCER COUNTY, Pennington, head of Shabakunk Creek, *B. Long 50136* (PH); MONMOUTH COUNTY, ca. 1 mi. NW of Cream Ridge, *B. Long 58552* (PH); MORRIS COUNTY, E shore of Lake Hopatcong, *P. H. Raven 16520* (KYO, MO); PASSAIC COUNTY, Passaic, *E. W. Berry in 1895* (NY); SALEM COUNTY, 1.5 mi. S of Sharptown, *J. Fogg 8840* (PH); SOMERSET COUNTY, Watchung, *H. N. Moldenke 1304* (DUKE, ILL, MO, PENN, PH); SUSSEX COUNTY, Beaver Lake, *K. K. Mackenzie 4326* (MO); UNION COUNTY, Watchung Reservation, *H. N. Moldenke 22455* (SMU); WARREN COUNTY, 0.5 mi. NE of Franksboro, *R. True 5726* (PENN). NEW YORK: ALBANY COUNTY, Rensselaerville, *G. R. Cooley 4771* (NO, VDB); ALLEGANY COUNTY, Allegany State Park, Tuna Valley, *W. Alexander in 1926* (US); BRONX COUNTY, Bronx Park, *G. Nash 315* (NY, PH); CATTARAUGUS COUNTY, Otto, *J. H. C. in 1881* (BH); CAYUGA COUNTY, Moravia, *C. Atwood in 1877* (CU); CHATAUQUA COUNTY, Lake Chatauqua, Bemis Point, *J. R. Churchill in 1896* (MO); CHEMUNG COUNTY, Elmira, S of Hoffman Nurseries, *L. H. Bailey 17316* (OKL, WTU); CHENANGO COUNTY, 5 mi. N of Norwich, *E. Davis 71* (NYS); CLINTON COUNTY, Valcour Island, *T. Baim & S. Smith 2993* (NYS); COLUMBIA COUNTY, Stuyvesant Falls, *R. McVaugh 1391* (PENN); CORTLAND COUNTY, S end of Chicago Bog, *A. Eames 6933* (CU, GH); DELAWARE COUNTY, Arkville, *E. Harvey in 1905* (PENN); DUTCHESS COUNTY, Hyde Park, Cardinal Road, *D. E. Boufford & H. E. Ahles 18836* (KYO, MO); ERIE COUNTY, Buffalo, Chautauqua, *M. Sawada 1030* (KYO, TNS); ESSEX COUNTY, woods near Minerva, *H. D. House 15402* (MO); GENESEE COUNTY, Oatka Creek valley, near Lime Rock, *W. A. Matthews 3147* (NCU); HAMILTON COUNTY, Indian Lake, *B. Lambert 82* (PH); HERKIMER COUNTY, along Graefenburg Res., *J. Haberer 2535* (GH); JEFFERSON COUNTY, Woodville, *H. D. House 19728* (NYS); KINGS COUNTY, Brooklyn, Prospect Park, *L. Stabler in 1886* (GH); LEWIS COUNTY, 2 mi. SW of Castorland, *N. Hotchkiss 2670* (NYS); MADISON COUNTY, Nelson, *F. Hunnewell 11711* (GH); MONROE COUNTY, 3 mi. W of Honeoye Falls, *W. A. Matthews 4360* (OKL, UC); NASSAU COUNTY, Albertson, Albertson Kettle-hole, *R. Abbott in 1952* (CU); NEW YORK COUNTY, Manhattan, Inwood Hell, *H. Dunslow in 1924* (NY); NIAGRA COUNTY, Lockport, *L. R. Moyer 2610* (MIN); ONEIDA COUNTY, woods bordering Delta Lake, *H. D. House 17911* (NYS); ONONDAGA COUNTY, De Witt, *C. A. Weatherby in 1915* (PH); ONTARIO COUNTY, Canandaigua, *E. J. Durand in 1891* (MIN); ORANGE COUNTY, Bear Mt. Area, *L. Y. Westra & L. S. Adderly 87* (KYO); ORLEANS COUNTY, 4 mi. W of Sweden Center, *F. R. Fosberg 48564* (US); OSWEGO COUNTY, Sandy Creek Township, *N. Hotchkiss 3153* (GH); OTSEGO COUNTY, Cooperstown, *F. Rane in 1919* (CU); QUEENS COUNTY, Alley Pond Park, *W. A. Weber 944* (COLO, ISC, OS); RENSSELAER COUNTY, margin of Glass Lake, *C. Brown 486* (LSU); RICHMOND COUNTY, Staten Island, Richmond, *O. Reich in 1906* (CU); ROCKLAND COUNTY, Ramapo Township, *J. Lehr 222* (NY); ST. LAWRENCE COUNTY, Canton, *O. Phelps 715* (CU, GH), Long Sault Lake, *E. Ogden et al. 54116* (NYS); SARATOGA COUNTY, Saratoga Lake, *H. D. House 26661* (POM); SCHOHARIE COUNTY, 2 mi. N of North Blenheim on hwy 30, *E. Haber 663* (TRT); STEUBEN COUNTY, W side of Waneta Lake, *R. Clausen 1370* (CU); SENECA COUNTY, Ovid, *J. Chickering in 1858* (US); SUFFOLK COUNTY, Long Island, Orient, *W. Ferguson 3891* (NY); SULLIVAN COUNTY, Wortsboro, *H. Eggert in 1873* (MO); TIOGA COUNTY, ca. 3 mi. SW of Owego on hwy 30, *E. Haber 646* (TRT); TOMPKINS COUNTY, near Blue Lake, *B. Maguire 6552* (POM, UTC, WS); ULSTER COUNTY, Marlboro, *J. Barnhart* 154 (NY); WARREN COUNTY, Northwest Bay on Lake George, *H. D. House 30119* (TEX); WASHINGTON COUNTY, Pilot Knob, Lake George, *H. D. House 28188* (TEX); WAYNE COUNTY, Savannah, Crusoe Prairie, *A. Wright & L. Griscom 10506* (CU); WESTCHESTER COUNTY, North Tarrytown, *J. Barnhart 1492* (NY); YATES COUNTY, Dresden, *W. S. Phillips 218* (ARIZ). NORTH CAROLINA: ALLEGHENY COUNTY, woodlands at junction of county routes 1405 & 1406, *S. W. Leonard et al. 1862* (ARIZ, B, BALT, BRY, CLEMS, DS, FUGR, KE, MONTU, NCU, NHA, NLU, UNCC, UTC, WCUH); ASHE COUNTY, Bluff Mountain, *G. E. Tucker 2931* (SMU, VDB); AVERY COUNTY, 1.3 mi. S of Linville on N.C. 105, *T. L. Mellichamp 413* (UNCC); BERTIE COUNTY, 3 mi. S of Merry Hill, *D. S. Correll 1963* (DUKE, NA); BUNCOMBE COUNTY, Biltmore, deep woods, *Biltmore Herb. 1968b* (GH, MICH, MIN, MO, NCSC, NCU, NY, NYS, OS, PENN, TUR, US, VT, W); BURKE COUNTY, Linville Gorge Camp at end of Wagon Road, *E. J. Alexander in 1923* (NCU); CABARRUS COUNTY, Egg Rock woods, *T. Daggy 4181* (NCU); CHEROKEE COUNTY, 2 mi. E of Andrews, *H. J. Oosting 34620* (DUKE); CRAVEN COUNTY, Croatan National Forest, Island Creek, *E. D. Cappel & R. K. Godfrey 137* (NCSC, UC); DAVIDSON COUNTY, 2.5 mi. W of Churchland, Boone's Cave, *A. E. Radford 12877* (NCU, UC); DURHAM COUNTY, ca. 2 mi. N of Weaver, tributary of Little R., *H. E. Ahles 58016* (NCU); FORSYTH COUNTY, Winston-Salem, *P. O. Shallert 324* (MO, NCU, OKL, UTC); GRAHAM COUNTY, Appalachian Trail, 0.25 mi. S of Stecoah Gap, *A. Jackson & D. Sather 002* (FUGR); GUILFORD COUNTY, tributary of Reedy Fork Creek near Summerfield, *L. Melvin in 1955* (NCU); HAYWOOD COUNTY, vicinity of Eagle's Nest near Waynesville, *P. C. Standley 5450* (US); HENDERSON COUNTY, Fraser Hollow–Lanning Creek, *D. Pittillo 436* (KY, OSC); HERTFORD COUNTY, Deep Swamp Branch, N of Lloyds Crossroads, *H. E. Ahles & J. A. Duke 45921* (NCU); IREDELL COUNTY, ca. 2.5 mi. S of Cool Spring off county road 2316, *M. G. Lelong 5927* (NLU); JACKSON COUNTY, 3 mi. NW of Glenville, Tuckaseegee Falls, *L. Anderson 1498* (PH); JONES

COUNTY, 5 mi. NE of Pollocksville, *M. N. Sears C426* (NLU); MACON COUNTY, 12 mi. W of Franklin, *W. B. Fox 4005* (BHO, NCSC, SMU, TENN); MADISON COUNTY, 4 mi. W of Hot Springs on U.S. 25-70, then 2.2 mi. S on Shut-In Creek Road, *H. E. Ahles & J. A. Duke 46466* (NCU, VPI); MARTIN COUNTY, near Conoho Creek 4.3 mi. NW of Williamston, *A. E. Radford 35284* (NCU, TENN, WVA); MCDOWELL COUNTY, Blue Ridge Parkway between Buck Creek Gap and Gillespie Gap, *J. H. Beaman 31* (NCSC); MECKLENBURG COUNTY, E of Mt. Holly–Huntersville Road, *J. F. Matthews & J. Hannon in 1972* (UNCC); MITCHELL COUNTY, 1.4 mi. NE of Hawk, *H. E. Ahles & J. A. Duke 47207* (GAS, NCU, UBC); ORANGE COUNTY, along creek below Mason Farm, *W. C. Coker in 1941* (NCU); PERQUIMANS COUNTY, 3 mi. N of Beach Spring, *A. E. Radford 5469* (MIN, NCU, PAC, PENN); PITT COUNTY, 1.2 mi. N of Grimesland, *A. E. Radford 35027* (MIN, NCU, RSA, SIU); POLK COUNTY, 4 mi. W of Tryon, *E. H. Walker 3462* (NCU, US); ROCKINGHAM COUNTY, Dan River near NC 14, S of Leaksville, *A. E. Radford 13670* (FSU, GA, GH, NCU, VDB); STOKES COUNTY, 2.2 mi. W of Harts Store, *A. E. Radford 37876* (COLO, NCU, OKLA); SURRY COUNTY, Pilot Mt., *H. R. Totten in 1935* (NCU); SWAIN COUNTY, Nantahala Gorge, 1 mi. S of Talc Mt., *A. E. Radford & J. G. Haesloop 7236* (NCU); TRANSYLVANIA COUNTY, along Coontree Creek Trail 1 mi. from U.S. 276, *T. L. Mellichamp 854* (UNCC); WAKE COUNTY, W. B. Umstead State Park, *G. P. Sawyer, Jr. & H. E. Ahles 1454* (NCU); WARREN COUNTY, Poplar Mount, *W. D. Seaman 3457* (NCU); WATAUGA COUNTY, 2.3 mi. SW of Bethel, *H. E. Ahles & J. A. Duke 43869* (NCU); WILKES COUNTY, 5 mi. E of Moravian Falls, *A. E. Radford 15242* (NCU); YANCEY COUNTY, NC 197 near Little Cane River Gap, *A. E. Radford 45055* (ASU, CM, COLO, FSU, GA, GAS, GH, H, IND, ISC, KANU, KY, LL, MIN, NCU, NDA, NY, OKLA, OSC, PAC, RSA, SIU, SMU, TENN, UARK, UBC, UC, VDB, VPI, WIS, WVA). NORTH DAKOTA: BARNES COUNTY, Kathryn, *N. F. Bergman 994* (NDA, OKL, POM); BENSON COUNTY, Pleasant Lake, *J. Lunell in 1912* (NY, SDU, US); CASS COUNTY, Fargo, *N. F. Bergman 2318* (MIN, MO, NDA, SNU); GRIGGS COUNTY, 5.5 mi. N, 1 mi. W of Binford, Red Willow Lake, *G. E. Larson 3640* (NDA); MORTON COUNTY, Huff, *O. A. Stevens in 1954* (NDA); PEMBINA COUNTY, Cavalier, *O. A. Stevens 2134* (CAN, DAO, MIN, NDA, NLU, NY, UC, US); RANSOM COUNTY, Little Yellowstone Park, *G. Seiler 2174* (KANU, MO, NDA); RICHLAND COUNTY, Leonard, *O. E. Stevens 284* (DAO, GA, MIN, MT, NDA, NY, OKL, SMU, UC, WIS); WALSH COUNTY, 1 mi. N, 3 mi. W of Park River, *G. E. Larson 3482* (KANU, NDA). OHIO: ADAMS COUNTY, Mineral Springs, *W. A. Kellerman in 1900* (OS); ASHLAND COUNTY, Jackson Township, 4 mi. SE of Sullivan, *G. T. Jones 69-7-23-817* (FSU); ASHTABULA COUNTY, Windsor Township, Wisell Road, 0.5 mi. S of U.S. rte 322, *L. W. Tandy 654* (VDB); ATHENS COUNTY, Athens Township, *H. Moore 1517* (BHO); AUGLAIZE COUNTY, St. Mary's, *A. Wetzstein in 1896* (OS); BELMONT COUNTY, Barnesville, *E. E. Laughlin in 1910* (OS); BROWN COUNTY, Sardinia, *W. A. Kellerman in 1900* (OS); BUTLER COUNTY, Oxford, *L. O. Overholts in 1910* (MO); CARROLL COUNTY, Washington Township, intersection county rte 14 & twp rte 260, *A. W. Cusick 8215* (KE); CHAMPAIGN COUNTY, rte 68 N of Springfield, *L. D. Cribben 248* (BHO, OKL); CLARK COUNTY, Springfield, *F. Davidson in 1885* (OSC); CLINTON COUNTY, New Antioch, *J. S. Vandervort in 1892* (OS); COLUMBIANA COUNTY, Butler Township, SW¼ Sec. 20, *T. S. Cooperrider 6436* (KE); COSHOCTON COUNTY, North Appalachian Experimental Watershed, near Coshocton, *H. N. Moldenke 13138* (CM, NCSC, ND, OS, OSC, VDB); CRAWFORD COUNTY, Bucyrus Township, Wyandot Road, *A. W. Cusick 10264* (KE); Cuyahoga County, NW of Oakwood, *J. F. Reilly 69* (KE); DARKE COUNTY, S of Versailles, *L. Camp & C. Weishaupt in 1955* (OS); DEFIANCE COUNTY, Washington Township, Scott Road, W of U.S. rte 127, *A. W. Cusick 12067* (KE); DELAWARE COUNTY, near tile works, *R. Crane 2952* (FSU, SMU, TRT); ERIE COUNTY, by Green Road, 1.5 mi. SE of Birmingham, *G. T. Jones 67-6-22-554* (BHO); FAIRFIELD COUNTY, Wahkeena Nature Preserve, *L. R. Noblick 419* (OS); FAYETTE COUNTY, Madison Mills, *E. D. Coberly & J. P. Song in 1901* (OS); FRANKLIN COUNTY, Alton-Darby Creek Road and Cole Road, *D. Keil 9332* (NLU, OS, VDB); FULTON COUNTY, Delta, *M. G. Aumend in 1892* (OS); GALLIA COUNTY, Raccoon Township, 0.5 mi. W of Tycon Lake, *G. M. Silberhorn 2756* (KE); GEAUGA COUNTY, Chardon Township, 3 mi. W of Chardon at Stebbins Gulch, *W. D. Hawver 61* (KE); GREENE COUNTY, John Bryant State Park, Yellow Springs, *D. Demaree 11437* (DS, MIN, NY, OS, SMU, UC, US); HAMILTON COUNTY, College Hill, *W. H. Aikeu in 1897* (OS); HANCOCK COUNTY, Blanchard Township, along Ottawa Creek, *A. W. Cusick 12009* (KE); HARDIN COUNTY, Jackson Township, ca. 1 mi. W, 0.5 mi. S of Forest, *C. Weishaupt in 1957* (OS); HENRY COUNTY, Harrison Township, adjacent to Hoy Cemetery, *A. W. Cusick 11855* (KE); HIGHLAND COUNTY, Brush Township, *F. Bartley in 1932* (BHO); HOCKING COUNTY, Little Rocky, E of Gibisonville, *J. D. & W. A. Westendahl 741* (BHO); HOLMES COUNTY, Killbuck Township, above Killbuck Creek, *T. S. Cooperrider 8169* (KE); HURON COUNTY, NE corner of Wakeman Township, *G. T. Jones in 1964* (KE); JACKSON COUNTY, Lake Alma State Park, *D. E. O'Dell 768* (BHO); JEFFERSON COUNTY, Island Creek Township, Granater Farm, *A. W. Cusick 8192* (KE); KNOX COUNTY, Jefferson Township, Mohican R., *P. L. Pusey 1155* (KE); LAKE COUNTY, Mentor, marsh of Wilson Street circle, *L. W. Tandy 679* (VDB); LAWRENCE COUNTY, Washington Township, N part of township, *C. Weishaupt in 1956* (OS); LICKING COUNTY, St. Albans Township, ca. 1 mi. N, 0.5 mi. E of Alexandria, *C. Weishaupt in 1957* (OS); LOGAN COUNTY, Union

Township, above Ruby Lake, *A. W. Cusick 13394* (KE); LORAIN COUNTY, Brownhelm Township, Chance Creek ravine, *T. S. Cooperrider & E. Herrick 7211* (KE); LUCAS COUNTY, oak openings, *R. E. Shanks in 1937* (OS); MADISON COUNTY, London, *Mrs. K. D. Sharp s.n.* (OS); MAHONING COUNTY, Green Township, W of Egypt Road, between rte 165 and Columbiana Co. line, *C. F. Chuey 797* (BHO); MEDINA COUNTY, Liverpool Township, SE of Valley City, *G. T. Jones 73-6-24-662* (TENN); MEIGS COUNTY, Forked Run State Park, Area 1, *J. D. Westendahl 63-177* (BHO); MONROE COUNTY, Summit Township, rte 78, 0.25 mi. E of Twp rte 41, *A. W. Cusick 9392* (KE); MONTGOMERY COUNTY, Dayton, *H. Saske in 1894* (OS); MORGAN COUNTY, Deerfield Township, NW¼, Sec. 3, *G. M. Silberhorn 1742* (KE); NOBLE COUNTY, Sharon Township, *W. A. Kellerman et al. in 1896* (OS); OTTAWA COUNTY, Put-in-Bay, *R. B. Clarkson in 1958* (WVA); PICKAWAY COUNTY, woods, *R. R. Dreisbach 2610* (MICH); PIKE COUNTY, Road S of Omega, *G. S. Crowl in 1938* (OS); PORTAGE COUNTY, 0.3 mi. S of the Geauga Co. line on rte 306, *D. E. Boufford 18819* (BM, CM, DS, E, G, K, KYO, LD, MHA, MO, NCU, PE, SHIN); PREBLE COUNTY, Hueston's woods N of Oxford, *E. B. in 1934* (DAO); Putnam County, Union Township, Sec. 16, *C. Weishaupt in 1960* (OS); RICHLAND COUNTY, Mansfield, *C. Wilkinson 3363* (BHO, CM, CU, DUKE, NMC, OKL, OS, RM, WIS); ROSS COUNTY, Mt. Logan near Chillicothe, *G. W. Hall 448* (BHO); SANDUSKY COUNTY, Sandusky-Riley Township, *C. Weishaupt in 1956* (OS); SCIOTO COUNTY, Shawnee State Forest, Friendship, Camp Gordon, C.C.C., *D. Demaree 10758* (CM, DS, GH, MIN, MO, OS, PH, UC, US, WIS); SENECA COUNTY, Thompson Township, 3 mi. W of Flat Rock, *G. T. Jones 69-7-9-703* (KE); SHELBY COUNTY, Botkins, *S. E. Harlacher in 1905* (OS); STARK COUNTY, Lake township, NE¼, Sec. 19, *J. E. Mann 859* (KE); SUMMIT COUNTY, SW of Everett, Bath Township, *G. T. Jones 73-7-10-769* (OS); TRUMBULL COUNTY, Casey's Spring along Mill Creek, *D. E. Boufford 18821* (CM, K, KYO, MHA, MO, NCU); TUSCARAWAS COUNTY, Wayne Township, 2 mi. N of Dundee, *B. Andreas 194* (KE); VAN WERT COUNTY, Ridge Township, *M. B. Overholt in 1940* (OS); VINTON COUNTY, Zaleski State Forest, King Hollow Trail, *L. V. Mingrone 406* (BHO, NLU); WASHINGTON COUNTY, Lawrence Township, near junction of rte 26 & road 25, *G. M. Silberhorn 1942* (KE); WAYNE COUNTY, Milton Township, intersection of State rte 604 & County rte 44, *A. W. Cusick 2688* (KE); WILLIAMS COUNTY, Brady Township, Shilling Farm, *A. W. Cusick 13661* (KE); WOOD COUNTY, Liberty Township, Sec. 21, *R. E. Shanks in 1937* (OS). OKLAHOMA: CADDO COUNTY, near Hinton, Devil's Canyon, *G. W. Stevens 938* (DS, GH, ILL, MIN, MO, NY, OKL, OKLA, US); CHEROKEE COUNTY, 0.5 mi. S of junction State hwy 10 on Chewey Road, *J. & C. Taylor 24767* (DUR), Eagle's Bluff, 12.2 mi. NE of Tahlequah on State 10, *C. S. Wallis 798* (OKLA); LEFLORE COUNTY, ca. 5.5 mi. NE of Big Cedar, N facing side of Rish Mt., *J. & C. Taylor 24653* (DUR); OTTAWA COUNTY, 5.5 mi. E of Miami on State 10, valley of a creek on Spring R., *C. S. Wallis 7322* (BH, GA, GH, KANU, NCU, NO, OKL, OKLA, SMU, TEX, UARK, UC). PENNSYLVANIA: ADAMS COUNTY, 1 mi. W of Heidlersburg, *H. I. Kennedy 700* (WVA); ALLEGHENY COUNTY, Pittsburgh, *W. C. Grimm 75* (CM); ARMSTRONG COUNTY, N side of the village of Baum, *D. E. Boufford 18824* (BM, KYO, MHA, MO); BEAVER COUNTY, woods along Beaver-Conway Road, *L. K. Henry 999* (NLU); BEDFORD COUNTY, W rim, Wolf Swamp Watershed, *H. Duppstadt in 1970* (WVA); BERKS COUNTY, Oley Furnace, S slope of Sheep Hill, *H. Wilkins 2887* (ND); BLAIR COUNTY, 3.4 mi. SE of Williamsburg, *L. K. Henry in 1957* (CM); BRADFORD COUNTY, *E. Bartram in 1913* (PH); BUCKS COUNTY, Argus, *W. Benner in 1908* (ORE); BUTLER COUNTY, McBride, *W. E. Buker in 1963* (CM); CAMBRIA COUNTY, 0.25 mi. NE of Nicktown, *H. Kline in 1951* (CM); CAMERON COUNTY, Miller, *O. E. Jennings in 1904* (CM); CENTRE COUNTY, 3 mi. SE of Philipsburg, *L. K. Henry in 1941* (CM); CHESTER COUNTY, 2 mi. E of Eagle, *L. K. Henry in 1967* (CM); CLARION COUNTY, Red Bank, *O. E. Jennings in 1904* (CM); CLEARFIELD COUNTY, E of Clearfield, *O. E. Jennings in 1908* (CM); CLINTON COUNTY, 2 mi. N of Gleasonton, *L. K. Henry in 1956* (CM); COLUMBIA COUNTY, near Lanbach Station, *H. Meredith in 1920* (PH); CRAWFORD COUNTY, 2 mi. NE of Geneva, *R. C. Leberman in 1963* (CM); CUMBERLAND COUNTY, 2.5 mi. SW of Huntsdale, *E. T. Wherry in 1961* (PENN); DAUPHIN COUNTY, Dauphin, *J. K. Small in 1888* (US); DELAWARE COUNTY, Crum Creek, *W. Stone 1489* (UTC); ELK COUNTY, Benezette Township, Dent's Run, *A. N. Rood & W. Simon 2729* (KE); ERIE COUNTY, Presque Isle, *W. R. Van Dersal 1857* (CM); FAYETTE COUNTY, 2.5 mi. NE of Summit, *E. H. McClelland in 1923* (CM); FRANKLIN COUNTY, Mount Alto Forest, *R. H. True 12* (CM); FULTON COUNTY, N Ft. Littleton interchange of the Pa. Turnpike, *W. E. Buker in 1969* (CM); GREENE COUNTY, 3 mi. SE of Ryerson, *L. K. Henry & W. E. Buker in 1954* (CM); HUNTINGDON COUNTY, 0.5 mi. S of Valley School, *W. F. Westerfeld 8942* (BALT); INDIANA COUNTY, 2 mi. S of Uniontown, along rte 580, *W. E. Buker in 1974* (CM); JEFFERSON COUNTY, Allen Mills, 3.6 mi. N of rte I-80 on rte 310, *D. E. Boufford 18828* (CM, KYO, MHA, MO, PE); JUNIATA COUNTY, 2 mi. NW of Oakland Mills, *H. A. Wahl et al. 13836* (PENN); LACKAWANA COUNTY, 0.5 mi. NW of Wallsville, *S. Blowenke 8069* (PENN); LANCASTER COUNTY, 1 mi. NE of Cocalico, *R. Schaeffer, Jr. 43580* (KANU); LAWRENCE COUNTY, 1 mi. W of Eastbrook, along Neshannock Creek, *L. K. Henry & F. H. Beer in 1950* (CM); LEBANON COUNTY, 3 mi. SW of Schaefferstown, *C. S. Keener 551* (CM); LEHIGH COUNTY, Bethlehem, Lehigh Mt., *J. A. Wolle, in 1841* (CM); LUZERNE COUNTY, 0.25 mi. NNW of Nescafeck, *S. Glowenke 2719* (PENN); LYCOMING COUNTY, Williamsport to Allenwood, *O.*

E. Jennings in 1908 (CM); MCKEAN COUNTY, 5 mi. N of Port Allegany, *L. K. Henry in 1956* (CM); MERCER COUNTY, 8 mi. NW of Mercer, Shenango Reservoir, *L. K. Henry in 1967* (CM); MIFFLIN COUNTY, 3 mi. NW of Milroy, *J. M. Fogg 15491* (PENN); MONROE COUNTY, near Bushkill, Little Bushkill Creek, *F. B. Buser 10807* (NLU); MONTGOMERY COUNTY, road to Mason's Dam, *V. Wismer 422* (MIN); MONTOUR COUNTY, 2.3 mi. NW of Danville, *Wade & Wade 1813* (PAC, PENN); NORTHAMPTON COUNTY, Easton, Chestnut Hill, *O. E. & G. K. Jennings in 1920* (CM); NORTHUMBERLAND COUNTY, 0.75 mi. SE of Mandeta, *E. T. Wherry in 1961* (PENN); PERRY COUNTY, 1.5 mi. NW of New Bloomfield, *J. W. & M. T. Adams 2083* (CU, MO); PHILADELPHIA COUNTY, near Philadelphia, *F. Ball in 1881* (MO); PIKE COUNTY, near Milford, *R. Little in 1941* (CM); POTTER COUNTY, near Ole Bull State Park along rte 144, *W. E. Buker in 1965* (CM); SCHUYLKILL COUNTY, 0.25 mi. S of Schuylkill Haven, *P. R. Wagner 7453* (CM); SNYDER COUNTY, 3 mi. SW of Beversprings, *Wade & Wade 1418* (PENN, WIS); SOMERSET COUNTY, woods at Murdock, *L. K. Henry & D. Ross in 1963* (CM); SULLIVAN COUNTY, Eaglesmere, *T. Githens in 1945* (PENN); SUSQUEHANA COUNTY, 2 mi. NNW of Elkdale, *J. M. Fogg 12144* (PENN); UNION COUNTY, 4 mi. W of Turtleville, Shamokin Mt., *O. B. Reed in 1949* (WVA); VENANGO COUNTY, 2.5 mi. NW of Reno, *L. F. Baltzell 5-90* (FSU); WARREN COUNTY, North Warren, *H. N. Moldenke 16599* (WVA); WASHINGTON COUNTY, 2.5 mi. from the County Fairgrounds near Washington, Andy Farm, *D. Wilson 28* (CM, WVA); WAYNE COUNTY, Waymart, Moosie Mt., *E. M. Gress et al. in 1920* (CM); WESTMORELAND COUNTY, Rodney, 8 km W of the Donegal interchange on the Pa. Turnpike, *P. Busey 206* (MO); YORK COUNTY, 2 mi. W of Wellsville, *K. B. Hoover 3979* (NCU). RHODE ISLAND: NEWPORT COUNTY, Middletown, *M. Simmons in 1898* (NEBC); PROVIDENCE COUNTY, near Diamond Hill, *E. J. Palmer 46761* (KY); WASHINGTON COUNTY, Hopkinton, N of Ashaway, *M. L. Fernald et al. in 1919* (NEBC), Block Island, *R. Marles 96* (NEBC). SOUTH CAROLINA: DARLINGTON COUNTY, along E side of Lauther's Lake on Witherspoon Island, *B. E. Smith 599* (NCU); OCONEE COUNTY, Brasstown Creek, gorge below the confluence with Little Brasstown Creek, *D. E. Boufford & J. R. Massey 17014* (NCU, UNCC); PICKENS COUNTY, Eastatoe Creek ca. 1 mi. above where it crosses hwy 178, *C. L. Rodgers & G. Shiflet, Jr. 69408* (FUGR). SOUTH DAKOTA: BENNETT COUNTY, LaCroft, *S. S. Visher 2237* (SDU); CLAY COUNTY, Vermillion, *W. H. Over 15832* (RM); GRANT-ROBERTS COUNTIES, SW shore of Big Stone Lake, Scout Camp, *P. Johnson 99* (GH, IA, ISC, MICH, MO, MONTU, NY, TEX, UMO, WTU); LAWRENCE COUNTY, Whitewood, *W. H. Over 13883* (SDU); PENNINGTON COUNTY, near Dark Canyon, along Rapid Creek, *A. C. McIntosh 528* (RM, SDU); ROBERTS COUNTY, Big Stone Lake, 2 mi. E of Hartford Beach, *B. Boivin 13831* (DAO, SASK); TODD COUNTY, 10 mi. SW of Roseland, Ironwood Creek valley, *W. L. Tolstead 4-386* (ISC). TENNESSEE: ANDERSON COUNTY, Melton Hill Reservoir, S of Solway Bridge, *W. H. Ellis 28853* (GA, TENN); BLEDSOE COUNTY, vicinity of Low Gap, *R. E. Shanks et al. 4463* (TENN); BLOUNT COUNTY, Walland, *L. E. Wehmeyer 270* (MICH); CARROLL COUNTY, NE of McMinnville, *R. E. Shanks et al. 5110* (TENN); CARTER COUNTY, woods in Sinking Creek area, *J. Pearman in 1955* (TENN); COFFEE COUNTY, Sinking Pond forest on AEDC land E of Tullahoma, *N. DeSelm et al. in 1973* (TENN); CUMBERLAND COUNTY, Black Mt., *N. E. Mullens in 1950* (FUGR); DAVIDSON COUNTY, 14.6 mi. from Peabody, *J. M. Shaver 8534* (SMU, TENN, VDB); FENTRESS COUNTY, S of Jamestown, rim of Buffalo Cove, *R. E. Shanks et al. 4058* (TENN); FRANKLIN COUNTY, N of Sherwood, *H. Eggert in 1897* (MO); GRAINGER COUNTY, Lea Lakes, *A. J. Sharp & L. R. Hesler 1607* (ND, TENN, UMO); GREENE COUNTY, ca. 0.5 mi. N of the French Broad R. along Paint Creek, *D. E. Boufford et al. 18111* (MO); GRUNDY COUNTY, just S of Beersheba Springs, *Dr. & Mrs. A. J. Sharp et al. 43575* (NCU, NY, VDB); HAWKINS COUNTY, Stanley Valley, *J. Wolfe 18389* (TENN); HAYWOOD COUNTY, Forked Deer (P.O.), *S. M. Bain 45* (OS); HENRY COUNTY, 1.5 mi. NE of Jones Mill, C. Boyd Farm, *D. H. Webb in 1974* (MUR); HICKMAN COUNTY, 1.5 mi. N of Nunnelly, *R. Kral 53703* (VDB); HOUSTON COUNTY, 4 mi. SE of Tennessee Ridge, *A. Clebsch in 1956* (NCU); KNOX COUNTY, Knoxville, Cherokee Bluffs, *H. M. Jennison in 1928* (MO, OKL); LAUDERDALE COUNTY, creek bottom W of Halls, *A. J. Sharp et al. 7968* (TENN); LAWRENCE COUNTY, NW of St. Joseph, Ted Smith Farm, *A. J. Sharp et al. 18* (RSA, TENN); LOUDON COUNTY, near Martel, *G. Jones & F. Wargo 4106* (NY); MONTGOMERY COUNTY, U.S. 41W, just E of Clarksville, *J. M. Shaver 9253* (VDB); OBION COUNTY, ca. 2 mi. E of Lassiter Corner along State hwy 21, *D. H. Webb et al. 915* (TENN); ROANE COUNTY, Clinch River Breeder Reactor site, *S. F. Hale & F. E. Williamson 48784* (TENN); RUTHERFORD COUNTY, Snail Shell Cave, 1.9 mi. NE of Rockvale, *L. E. Franklin et al. 276* (VDB); SEVIER COUNTY, Great Smoky Mountains National Park, ca. 0.5 mi. beyond Sugarlands, *K. E. Rogers 43620* (TENN); SULLIVAN COUNTY, Piney Flats, *A. J. Sharp 22364* (TENN); SUMNER COUNTY, ca. 3 mi. S of Westmoreland, *R. Kral 56103* (VDB); UNICOI COUNTY, Tennessee–North Carolina state line along the Appalachian Trail, *D. Norris & D. Frodin 33072* (TENN); WASHINGTON COUNTY, Johnson City, Cherokee Mt., *N. McCarroll & A. J. Sharp 3838* (TENN); WAYNE COUNTY, Natchez Trace Parkway, *W. McDougall 1373* (US); WHITE COUNTY, N of Yankeetown, *A. J. Sharp et al. 11572* (TENN); WILLIAMSON COUNTY, Fernvale, ca. 3 mi. W, *E. Quartermann 5083* (VDB). VERMONT: ADDISON COUNTY, Bristol, *C. H. Knowlton in 1937* (TENN); BENNINGTON COUNTY, Winhall, *E. T. & H. N. Moldenke 9957* (BH, CM, ILL, MO, NA, NY); CALEDONIA COUNTY,

Ryegate, rte 302, *F. C. Seymour 18952* (MO); CHITTENDEN COUNTY, Richmond, rte 2 near Bolton line, *F. C. Seymour 22344* (MO, SMU); ESSEX COUNTY, Concord, *A. S. Pease 28459* (NEBC); FRANKLIN COUNTY, Swanton, *C. H. Knowlton, Plantae Exsiccatae Grayanae 571,* distributed as *C. canadensis* (= *C.* × *intermedia* Ehrh.), see also under *C.* × *intermedia* (CAN, VT); GRAND ISLE COUNTY, Grand Isle, *C. H. Knowlton in 1935* (NEBC); ORANGE COUNTY, Bradford, Wright's Mt., *E. Sundell 1283* (ASU); ORLEANS COUNTY, Willoughby, Fern Cave, *A. Lorenz in 1898* (NEBC); RUTLAND COUNTY, Brandon, *D. L. Dutton in 1921* (CM, CU, MO); WASHINGTON COUNTY, Montpelier, *C. H. Knowlton in 1915* (NEBC); WINDHAM COUNTY, Vernon, *B. L. Robinson 111* (NEBC); WINDSOR COUNTY, Bethel, *L. M. Kutchka in 1946* (CM). VIRGINIA: ALBERMARLE COUNTY, Keene, *C. E. Stevens 1128* (FARM); ALEXANDRIA COUNTY, above Pimmitt's Run at Chain Bridge, *N. Hotchkiss 1425* (?); AMELIA COUNTY, no further data, *J. B. Lewis 127* (VPI); AMHERST COUNTY, Blue Ridge Parkway, Otter Creek Trail between Concession & Otter Lake, *R. S. Freer & D. Ochsner in 1965* (LYN, VPI); APPOMATTOX COUNTY, near Stonewall Creek on County road 613, *G. W. Ramsey et al. 6622* (LYN, NCU, VPI); ARLINGTON COUNTY, vicinity of Fort Scott, *C. O. Erlanson 192* (DAO); CITY OF ARLINGTON, *F. Blanchard in 1890* (MO); AUGUSTA COUNTY, trail from White Rock Gap on Blue Ridge Parkway to Sherando Campgrounds, *R. S. Freer & J. Rockwell 4222* (LYN, NCU, VPI, WILLI); BATH COUNTY, 7 mi. W of Warm Springs on Va. 39, *O. W. Gupton 4027* (NCU, UNCC, WCUH); BEDFORD COUNTY, SW of Visitor Center, Peaks of Otter, *R. S. Freer 2744* (GH, LYN, VPI); BLAND COUNTY, 3 mi. SE of Suiter, *R. Kral 10883* (NCU, SMU, VPI); BOTETOURT COUNTY, W slope of Flat Top Mt., *R. S. Freer 1638* (GH, LYN); BRUNSWICK COUNTY, (see synonomy under *C. lutetiana* subsp. *canadensis*); BUCHANAN COUNTY, open slope near Council, *A. M. Harvill 34540* (FARM); BUCKINGHAM COUNTY, N of Bat Creek, *A. M. Harvill 17141* (MO, NCU); CAMPBELL COUNTY, 4.5 mi. S of Lynchburg on rte 29, *G. S. Waggoner & W. F. Ruska 8262* (LYN); CAROLINE COUNTY, between Mount Creek & Rappahannock Academy, *T. Bradley & I. Miller 12343* (GMUF); CHARLES CITY COUNTY, Harrison Lake National Fish Hatchery, *D. M. E. Ware 4269* (NCU, WILLI); CHARLOTTE COUNTY, creek near Staunton R. on county road 746, just S of county road 750, *G. W. Ramsey et al. 9166* (LYN); CLARKE COUNTY, Blandy Experimental Farm, Boyce, *J. T. Baldwin 5223* (VPI); CULPEPPER COUNTY, N slope of Mt. Pony, *H. A. Allard 8961* (VPI); DICKENSON COUNTY, ca. 10 mi. S of Haysi, *R. Kral 13060* (VPI); DINWIDDIE COUNTY, E of Dinwiddie, *M. L. Fernald & B. Long 10750* (GH, PH); ESSEX COUNTY, Hunter Mill Campground, *Miller & Stanley in 1974* (GMUF); FAIRFAX COUNTY, between rte 698 and Wedderburn Road, *J. Joosten 41* (FARM); FAUQUIER COUNTY, 2 mi. N of Hopewell Gap, *H. A. Allard 1836* (CM, GH, MO, NY); FLOYD COUNTY, Floyd, *W. Lord 102* (LYN); FLUVANNA COUNTY, near E Fork Kent Branch, 75 yards from the junction with the Middle Fork, *G. M. Diggs, Jr. & D. Soltis 279* (WILLI); FRANKLIN COUNTY, junction of county roads 748 & 788, *G. W. Ramsey et al. 6712* (LYN, NLU); FREDERICK COUNTY, Star Tannery, *F. W. Hunnewell 12412* (VPI); GILES COUNTY, 3 mi. W of Eggleston, Buckeye Mt., *G. B. Straley 1140* (MO); GLOUCESTER COUNTY, Clay Bank, on Berg Farm, rte 616, *M. H. Berg 267* (BALT, FUGR, NCU); GRAYSON COUNTY, 1 mi. NE of Corners Rock, *A. M. Harvill et al. 33631* (FARM); GREENE COUNTY, Shenandoah National Park, vicinity of Pinefield Lean-to, *J. Ewan 17229* (DUKE, NO); HALIFAX COUNTY, 2 mi. S of Brookneal, Staunton R. on hwy 501, *G. W. Ramsey et al. 4150* (LYN, NCU, VPI); HENRY COUNTY, near Philpott, near Smith R., *C. E. Stevens 13242* (FARM); HIGHLAND COUNTY, ca. 4 mi. S of McDowell, W. Va., *K. A. Nicely 730* (NCSC, NCU, VPI); JAMES CITY COUNTY, College of William & Mary, N section of Squirrel Point, *A. Barars 257* (NCU, VDB); KING WILLIAM COUNTY, S of Epworth on rte 610, *T. Bradley 13107* (GMUF); LEE COUNTY, Lovelady Gap, *B. J. & A. M. Harvill 31818* (FARM); LOUDOUN COUNTY, Upperville, *F. W. Hunnewell 10675* (VPI); LUNENBURG COUNTY, N Meherrin R., approx. 1 mi. from intersection with county road 689, *G. W. Ramsey et al. 9487* (LYN); CITY OF LYNCHBURG, Blackwater Creek just E of Langhorne Road, *G. W. Ramsey 15742* (LYN); MADISON COUNTY, along Five Tower Road just off county road 649, *F. C. James 11420* (NCU); MATHEWS COUNTY, S of Soles, N End Branch, *E. T. Wherry & F. W. Pennell 12609* (MO, NY); MECKLENBURG COUNTY, W hillside of Meherrin R. valley of Va. 664, *W. D. Seaman 4150* (NCU); MIDDLESEX COUNTY, 0.1 mi. S of rte 618 and 1.5 mi. W of its intersection with rte 17, *E. Train 314* (WILLI); MONTGOMERY COUNTY, ca. 3 mi. W of Price's Fork, *R. Kral 14813* (VDB); NANSEMOND COUNTY, Suffolk, *H. A. Gleason 8601* (NY); NELSON COUNTY, Tye R. near intersection of county roads 662 & 739, *G. W. Ramsey et al. 9331* (LYN, NCU); NEW KENT COUNTY, just E of rte 30, 0.5 mi. from its junction with rte 168, *D. Soltis & G. Hammond 283* (BALT, NCU, WILLI); CITY OF NEWPORT NEWS, Fort Eustis, NE side of loop at end of Stillwell Street, *P. K. Appler & S. Godwin 680* (NCU, WILLI); NORFOLK COUNTY, near Ocean View, *T. Kearney 1468* (US); NORTHUMBERLAND COUNTY, near Wicomico Church, *C. E. Stevens 13696* (FARM); NOTTOWAY COUNTY, Crystal Lake near Nottoway, *B. J. & A. M. Harvill 21795* (FARM); PAGE COUNTY, Stony Man Mt., near Luray, *E. S. & Mrs. Steele 69* (MO, US); PATRICK COUNTY, along county road 704 on Smith R. at bridge, *G. W. Ramsey et al. 6780* (LYN, NCU); PITTSYLVANIA COUNTY, Staunton R. on hwy 29 across from Altavista, *G. W. Ramsey et al. 4848* (LYN, NCU); POWHATAN COUNTY, rte 614, 0.67 mi. E of rte 613, *C. M. Corcoran & G. M. Diggs, Jr. 850* (WILLI); PRINCE EDWARD COUNTY, county road 625, 1.25 mi. E of the county line,

G. W. Ramsey et al. 7833 (LYN, NCU); PRINCESS ANNE COUNTY, Little Neck, *M. L. Fernald & B. Long 4069* (GH, PENN); PULASKI COUNTY, no further data, *H. B. Meredith in 1923* (POM); RAPPAHANOCK COUNTY, Shenandoah National Park, Buck Hollow Trail, *E. H. Walker 2424* (US); ROANOKE COUNTY, 2.4 mi. S of Wabun, Poor Mt., *L. J. Uttal 6568* (LYN, NCU, VPI); ROCKBRIDGE COUNTY, Short Hills, *R. S. Freer 2675* (LYN, US, VPI); ROCKINGHAM COUNTY, George Washington National Forest, Hone Quarry, *G. F. Roe 1138-B* (WILLI); RUSSELL COUNTY, Beartown Mt., on Red Fork of Franklin Creek, *A. Shield in 1959* (VPI); SCOTT COUNTY, limestone bluff just S of Hill, *A. M. Harvill 31800* (FARM); SHENANDOAH COUNTY, Little Fort, Peters Mill Run bog, *L. Artz in 1965* (VPI); SMYTH COUNTY, Va. 601, 2.1 mi. S of 16, *L. J. Uttal 8878-B* (AUA, BALT, LYN, VPI); SPOTSYLVANIA COUNTY, Fredericksburg, Fall Hill, *H. Iltis 265* (SMU); STAFFORD COUNTY, 3 mi. E of Stafford, *A. M. Harvill & C. E. Stevens 29212* (FARM); SURRY COUNTY, S side of College Run near road 634 bridge, *L. Musselman et al. 4949* (ID, NCSC, NCU, NLU, VSC, WILLI); TAZEWELL COUNTY, ca. 9 mi. S of Tazewell, *R. Kral 10938B* (FSU, NCU, VDB); WARREN COUNTY, Shenandoah National Park, Fort Wyndham Rocks, *F. R. Fosberg 45651* (US); WYTHE COUNTY, Lower Rocks, Reed Creek, *J. K. Small in 1892* (MO); YORK COUNTY, 200 yards W of bridge over Navy railroad on N side of Yorktown Parkway, *E. D. Salle & L. Kean 314* (FUGR, WILLI). WEST VIRGINIA: BARBOUR COUNTY, 2 mi. S of Philippi, rte 250, *E. L. Core 5955* (WVA); BERKELEY COUNTY, on Back Creek at rte 9, *E. L. Core 5810* (WVA); BOONE COUNTY, Jarrell's Branch, *W. V. U. Botanical Expedition 619* (WVA, WVW); BRAXTON COUNTY, Sugar Creek S of Gassaway, *F. J. Boggs in 1953* (WVA); BROOKE COUNTY, woods of Bethany College Farm, *J. S. Bonar in 1958* (WVA); CABELL COUNTY, Pleasant Valley, *F. A. Gilbert 592* (CM, DUKE, GA, ILL, MICH, MIN, MO, MT, NHA, NY, OKL, PH, SMU, TENN, UMO, US, WIS); CALHOUN COUNTY, Pink, *R. Harris in 1933* (WVA); DODDRIDGE COUNTY, 3 mi. W of Ashley, *E. L. Core 5563* (WVA); FAYETTE COUNTY, old logging area near Thayer, *W. N. Grafton & C. McGraw in 1972* (WVA); GRANT COUNTY, Difficult Creek, *F. Moreland in 1965* (WVA); GREENBRIER COUNTY, Cales Mt., *E. E. Smith & D. Cole in 1947* (WVA); HAMPSHIRE COUNTY, Capon Lake, *F. W. Hunnewell 18193* (WVA); HANCOCK COUNTY, ca. 3 mi. from Weirton, *J. S. Bonar in 1958* (WVA); HARDY COUNTY, ca. 1.25 mi. E of Mathias, *L. W. Wilson in 1941* (WVA); HARRISON COUNTY, near Clarksburg, *W. J. Judy in 1934* (WVA); JACKSON COUNTY, Crow Summit, *J. R. Mckown in 1949* (WVA); JEFFERSON COUNTY, Harper's Ferry, *E. L. Greene in 1912* (NDG); KANAWHA COUNTY, woods back Harper's Ferry, *E. L. Greene in 1912* (NDG); KANAWHA COUNTY, woods back of Edgewood Golf Course, *L. Greenlee in 1934* (WVA); LEWIS COUNTY, E side of ridge above road to Orlando, *E. A. Bartholomew & D. Wilson in 1965* (WVA); MARION COUNTY, Valley Falls, *M. Sweeney in 1960* (WVA); MARSHALL COUNTY, 2 mi. W of Bellton, *E. L. Core 5326* (WVA); MCDOWELL COUNTY, Panther State Forest, *D. J. Music in 1961* (WVA); MERCER COUNTY, Athens, *W. R. Boggess 284* (SMU); MINERAL COUNTY, *M. Brown in 1951* (WVA); MINGO COUNTY, in forest near Birch, *E. E. Berkley 952* (MO); MONONGALIA COUNTY, Hillman Boy Scout Reservation, *G. M. Silberhorn 1131* (VDB); MORGAN COUNTY, 4 mi. S of Great Cacapon, *E. L. Core in 1937* (WVA); OHIO COUNTY, Wheeling, *G. Guttenberg in 1878* (CM); PENDLETON COUNTY, Spruce Knob, *W. A. Lunk in 1941* (WVA); POCAHONTAS COUNTY, 5 mi. SW of Cass, *R. B. & J. Clarkson 634* (MAK); PRESTON COUNTY, Cathedral State Park, *M. Brown in 1964* (WVA); RALEIGH COUNTY, Rock Creek, *J. Jarrell in 1970* (WVA); RANDOLPH COUNTY, rte 33 just SE of Ellamore, *G. B. Rossbach 1437* (CLEMS, WVA, WVW); RITCHIE COUNTY, Smithville, *V. Elliott in 1970* (WVA); SUMMERS COUNTY, Keeney's Knob, *W. B. Fox in 1939* (WVA); TAYLOR COUNTY, Boothsville, *G. E. Constable in 1959* (WVA); TUCKER COUNTY, along Location Road E of St. George, *R. B. Clarkson 1494* (WVA); TYLER COUNTY, Raven's Rock, *E. E. Berkley in 1930* (MO); UPSHUR COUNTY, no further data, *W. M. Pollock in 1897* (MO); WEBSTER COUNTY, no further data, *J. B. Hinkle in 1957* (WVA); WETZEL COUNTY, N of Littleton, *O. Haught 520* (WVA); WIRT COUNTY, bank of Reedy Creek near Palestine, *E. A. Bartholomew in 1948* (WVA); WOOD COUNTY, along a wooded road, *C. F. Millspaugh 300* (WVA); WYOMING COUNTY, no further data, *D. S. Evans in 1962* (WVA). WISCONSIN: ADAMS COUNTY, 2.5 mi. W of Arkdale, *R. T. Brown 92* (WIS); BROWN COUNTY, DePere, *T. Kellogg in 1888* (US); BUFFALO COUNTY, Fountain City, Eagle Bluff, *N. C. Fassett & L. Wilson 5272* (GH, MICH, WIS); CALUMET COUNTY, no further data, *O. W. Meyer in 1964* (WIS); CHIPPEWA COUNTY, Brumet Island State Park, *M. Johnson in 1961* (WIS); CLARKE COUNTY, Neilsville, Listeman Arboretum, *J. E. Purcham 501-64* (WIS); COLUMBIA COUNTY, Caledonia Township, up hill from Town Hall along 78, *D. E. Allen in 1945* (WIS); CRAWFORD COUNTY, 4 mi. S of Soldiers Grove, *R. Koch 4127* (NEB, OSC); DANE COUNTY, Univ. of Wisconsin Arboretum, *H. H. Iltis 27541* (MO, WIS); DOOR COUNTY, Peninsula State Park, 2.5 mi. NNE of Fish Creek, *H. R. Bennett in 1956* (CAS, RSA, UC, WTU); DUNN COUNTY, S of Elk Mound, *D. E. Meyer 257* (WIS); FOND DU LAC COUNTY, Fond du Lac County Park, *J. M. Gates 15* (WIS); FOREST COUNTY, 8 mi. SE of Crandon, *F. W. Stearns in 1946* (WIS); GRANT COUNTY, 3 mi. NW of Cassville, Nelson Dewey Memorial Park, *H. H. Iltis & J. Neess 6437* (WIS); GREEN COUNTY, Spring Grove Maple Woods, Sec. 29, T1N, R9E, *K. T. Harper 911* (UT); GREEN LAKE COUNTY, Marquette, *L. H. Shinners in 1938* (WIS); IOWA COUNTY, upper N slope of Blue Mound, *Hoover & Green 103* (KYO); JACKSON COUNTY, 5 mi. S of Merrilan, *D. F. Grether 6048* (WIS); JEFFERSON COUNTY, 2 mi. S of Sullivan,

Bark River Game Preserve, *G. V. Burger 66* (WIS); JUNEAU COUNTY, Blackhawk Island, Wisconsin R., *D. Bramschreiber in 1959* (WIS); LACROSSE COUNTY, Onalaska Township, Sec. 26, T17N, R7, *T. G. Hartley 1200* (US, WIS); LAFAYETTE COUNTY, Fayette, *L. S. Cheney in 1888* (WIS); LINCOLN COUNTY, Merril Township, Knight Lake, *F. C. Seymour 14530* (SMU); MANITOWAC COUNTY, Kiel, open woods near Cedar Lake, *N. C. Fassett & A. P. Hoffmann 18556* (MO, WIS); MARATHON COUNTY, 3 mi. SW of Hagarty, Eau Claire R. Park, *H. H. Iltis 20877* (WIS); MARINETTE COUNTY, bank of Peshtigo R., *C. O. Grassl in 1936* (MICH); MARQUETTE COUNTY, Sec. 1, T17N, R8E, *P. D. Sorenson 3276* (WIS); MILWAUKEE COUNTY, Glendale, 0.75 mi. W of Kletsch Park, *P. J. Salamun in 1969* (NLU, TUR); MONROE COUNTY, 7 mi. N of Tomah, *H. H. Iltis & G. K. Noamesi 6963* (WIS); OCONTO COUNTY, County Park on Oconto R., *R. A. & D. L. Schlising 996* (WIS); OUTAGAMIE COUNTY, Grand Chute, *F. C. Seymour 10257* (WIS); OZAUKEE COUNTY, ca. 3 mi. SE of Newburg, *W. W. Oppel et al.* 1315 (WIS, WS); PEPIN COUNTY, Lake Pepin, *O. Anderson 207* (WIS); POLK COUNTY, Park, St. Croix Falls, *N. C. Fassett in 1934* (DAO, GH, IA, KYO, MIN, NY, UC, WIS, WS); PORTAGE COUNTY, valley of the Wisconsin R. near Stevens Point, *L. S. Cheney 3546* (WIS); RACINE COUNTY, Racine, *S. C. Wadmond 3230* (MIN); RICHLAND COUNTY, ca. 5 mi. N of Boaz, J. Shelton Farm, *R. G. Koch 7253* (KANU, MUR, NCU, UT); ROCK COUNTY, Spring Valley Township, *E. W. Fell 57-814* (WIS); RUSK COUNTY, N of Strickland, Devil's Elbow, *N. C. Fassett et al. 19958* (MO, NY, WIS); ST. CROIX COUNTY, Apple R. Canyon, 2 mi. upstream from junction with St. Croix R., *N. Russell in 1948* (MIN, WIS); SAUK COUNTY, Devil's Lake State Park, *J. H. Zimmerman 1145* (WIS); SAWYER COUNTY, Pickeral Lake, *H. H. Iltis 20613* (WIS); SHAWANO COUNTY, Sec. 21, T26N, R17E, *R. Liesner 135* (WIS); SHEBOYGAN COUNTY, woods at Elkhart Lake, *E. A. Bourdo 28657* (NLU); TAYLOR COUNTY, island in Rib Lake, *O. Anderson 206* (OKLA, WIS); TREMPEALEAU COUNTY, Perrot Lake State Park, *T. S. & B. A. Cochrane 5285* (WIS); VERNON COUNTY, Chimney Rock, *B. Warnes & T. S. Cochrane 198* (WIS); WALWORTH COUNTY, Kettle Moraine State Forest, Whitewater Lake Recreation Area, *J. & C. Taylor 12064* (DUR, SMU); WASHBURN COUNTY, Minong, *C. Goessl 8524* (B, WIS); WASHINGTON COUNTY, Sec. 12, T9N, R18E, *M. Emmerick in 1960* (WIS); WAUKESHA COUNTY, between Hartland & Pewaukee, *I. Cull 1328* (WIS); WAUPECA COUNTY, Clintonville, *K. D. Rill in 1959* (WIS); WINNEBAGO COUNTY, Black Wolf Township, Kaspar's woods, *N. A. Harriman 5058* (WIS).

The only clear, non-overlapping character that can be used to separate *Circaea lutetiana* subsp. *canadensis* and subsp. *quadrisulcata* is the presence or absence of a minute setaceous bracteole at the base of the pedicel. *Circaea lutetiana* subsp. *canadensis* nearly always has the bracteole present. In general, *C. lutetiana* subsp. *canadensis* is larger throughout than subsp. *quadrisulcata* with the only obvious exception being in the length of the stamen filaments. Ascherson and Magnus (1870) were the first to point out the importance of bracteoles, and Hara (1939, 1952) has pointed out some less consistent differences, which are not always obvious in dried specimens. These include dark red (purple), glandular-pilose sepals, and pink petals in subsp. *quadrisulcata* and generally green, moderately glandular-pilose to glabrescent sepals, and white petals in subsp. *canadensis*. These characters are not mutually exclusive; plants with purple sepals are commonly found in North America and plants with green sepals can occasionally be found in Asia. Petal color is equally variable in plants from both parts of the world, but with a slightly greater tendency for Asian plants to have pink petals.

4b. Circaea lutetiana L. subsp. **quadrisulcata** (Maxim.) Asch. & Magnus, Bot. Zeitung (Berlin) 28: 787. 1870.—FIG. 9.

Circaea lutetiana L. forma *quadrisulcata* Maxim., Prim. Fl. Amur. 106. 1859.
Circaea quadrisulcata (Maxim.) Franchet & Savat., Enum. Pl. Jap. 1: 169. 1873.
Circaea mollis Siebold & Zucc. var. *maximowiczii* H. Lév., Bull. Acad. Int. Géogr. Bot. 22: 223. 1912. Based on *Circaea lutetiana* L. forma *quadrisulcata* Maxim.

Circaea maximowiczii (H. Lév.) Hara, J. Jap. Bot. 10: 598. 1934.
Circaea maximowiczii (H. Lév.) Hara var. *viridicalyx* Hara, J. Jap. Bot. 10: 600. 1934. TYPE: Korea, Province Keiki, Koryo, 2 September 1930, *T. Nakai* (TI, holotype).
Circaea maximowiczii (H. Lév.) Hara forma *viridicalyx* (Hara) Kitagawa, Fl. Manshur. 328. 1939.

Plants 1.5–8 dm tall. The stem glabrous or with a few, very sparse, falcately recurved hairs, 0.2–0.3 mm long, on the upper internodes; petioles, leaves and inflorescence pubescent as in the species but never with long, straight or slightly curved, patent hairs, 0.5–1 mm long. Leaves 4.5–12 cm long, 2–5 cm wide, narrowly to broadly ovate to, more commonly, oblong ovate. Petioles 1.5–5 cm long. The terminal raceme ca. 2.5 cm long at initiation of flowering, to 30 cm long at cessation of flowering; the lateral racemes 2–5 cm long at initiation of flowering, to ca. 20 cm long at cessation of flowering. Flowering pedicels 0.9–4(–5*) mm long, without a bracteole at the base. Fruiting pedicels 3–5(–6.3*) mm long. Buds 2.6–3.8 mm long, 1.1–1.5 mm thick just prior to anthesis, most commonly purple. Ovary 1.2–1.7 mm long, 0.8–1.3 mm thick at anthesis, obovoid to subglobose. Floral tube 0.6–1 mm long, ca. 0.2 mm thick at the narrowest point, funnelform. Sepals (1.3–)1.9–3.2(–3.5*) mm long, 1–1.7 mm wide, most commonly purple. Petals 1–2(–2.5*) mm long, 1.4–2.5 mm wide, commonly pink; the apical notch 0.4–1.2 mm deep, ⅓ to slightly more than ½ the length of the petal. Filaments 1.6–3.5 mm long; anthers 0.3–0.7 mm long, 0.3–0.5 mm thick. Style (1.8–)3.2–4.2 mm long; stigma 0.2–0.4 mm tall, 0.3–0.6 mm thick. Nectar secreting disc 0.2–0.6 mm tall, 0.5–1 mm thick. Mature fruit 2.2–3.8 mm long, 1.8–3(–3.4*) mm thick, pyriform to subglobose, broadly rounded at the apex, rounded, usually obliquely to the pedicel, with prominent ribs and deep sulci. Fruiting pedicels reflexed or recurved, often strongly so. Combined length of pedicel and mature fruit, (5.3–)6.5–8.5(–10*) mm long. * Measurements in plants from the Altai Mountains, U.S.S.R.

TYPE: U.S.S.R.?, Amur ("forma fructa 4-sulcata") *C. Maximowicz* (LE, lectotype, not seen; GH, K, P, 2 sheets, isolectotypes).

Distribution (Fig. 11): Cool-temperate, deciduous forests and transitional mixed deciduous-boreal forests. Central Far Eastern Asia in North and South Korea, northeastern China, and southeastern U.S.S.R.; Sakhalin; Hokkaido and Honshu (one collection), Japan; westward between 50° and 60° N. Lat. to the vicinity of Moscow, U.S.S.R.; northern Altai Mountains. From near sea level to ca. 1,500 m. Flowering, mid-June to mid-August and sporadically to early September.

Representative specimens examined:

U.S.S.R.

RUSSIAN S.F.S.R. Pskov, Velikoluzki, Romanova, *A. Andrejev in 1900* (MW); Nizhegorov, Pavlovsk, Gorbatovski, opposite Voronsova, *D. Averkiev & N. Czernova in 1927* (MW); Birsk, *M. B. in 1839* (P); Primorski, Khasan, Kedrovaya Reservation in the Kedrovaya R. valley, *V. Dvorakovskaja in 1973* (MHA); Minusinsk, Osnatjennaja, *Ehnberg & Hammarströrm 762* (H, LD, S, TUR); Vladivostok, near Sedanka, *S. J. Enander in 1926* (E); Voronezh, 50 km N of Voronezh, *S. Golitsin in 1960* (DS); along the Enisej valley, *M. M. Ilon et al. in 1931* (LE); Primorski, vicinity of Rardolnoye, *R. Karpisonova in 1952* (MHA); Bashkirskaya, Arkhangel'skaya District, Solontsy, Duorava, *A. Khokhrykov & M. Mazurenko in 1966* (MO); Orenburg, *J. Klinge in 1846* (LE); Amurensy, Char R., *V. Komarov in 1895* (BM, NY, TI, W); Omoso, Paludy valley, *V. Komarov in 1896* (LE); Kazan Province, near Yadrin, Sura R., *S. Korzshinsky in 1885* (MW); central Amur, St. Pojarkova, *S.*

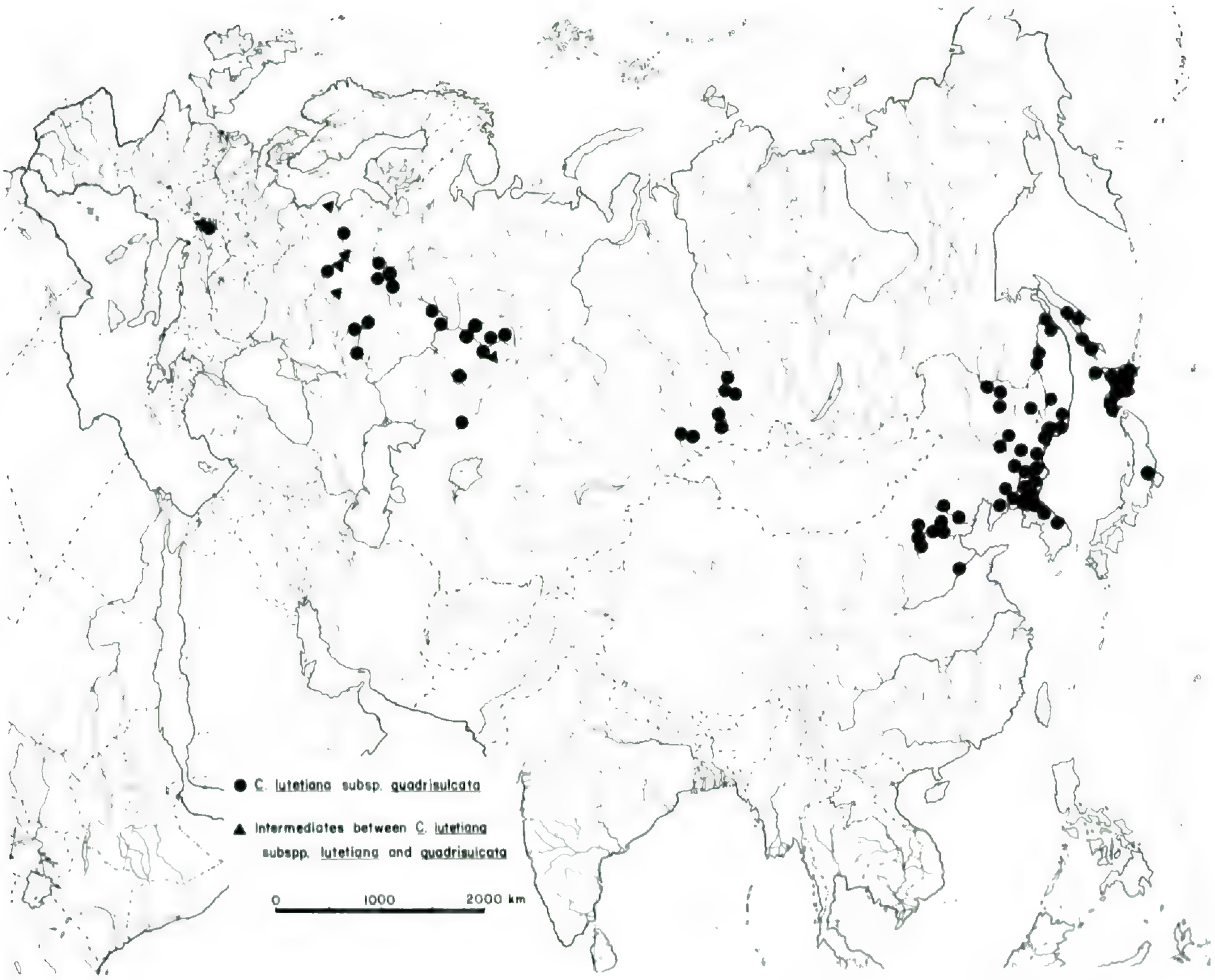


FIGURE 11. Distribution of *Circaea lutetiana* L. subsp. *quadrisulcata* (Maxim.) Asch. & Mag.

Korzshinsky in 1891 (GH, US); Kazan Province, Yadrin, *S. Korzshinsky in 1884* (ISC); Perm, Krasnoufimsk District, *S. Korzshinsky in 1887* (MW, UC); Moscow, Moscow District, Kuntzevo, *M. Koshevnikova in 1899* (G); eastern Sajan, Amil valley, *I. Krasnoborov in 1965* (LE); Tashbinsk District, Tashbin R., *I. Krasnoborov & L. Kurlina in 1966* (LE); Krasnoyarski Region, Shushenskaya, *I. Krasnoborov & M. Sukojan in 1964* (DAO); Krasnoyarski Region, Shushinsk District, *N. Leaborov & L. Gunderina in 1964* (LE); Korbekan at Amur R., *C. Maximowicz 1622* (BM, P); Vladimir Province, vicinity of Malenkovski, *M. Nasarov 4347* (MW); Ust'-Abakanskyi District, village of Trojakovo, *I. Neifeld & G. Vlasova in 1967* (LE); Ufa Province, Sterlitamak District, *I. V. & M. R. Novolokrovski & L. K. Mikhailov in 1926* (NY); Ufimskyi District, *I. V. Novolokrovski 1309* (LE); Rjazan, *P. P. Orlov in 1908* (MW); Kagan Province, village of Kozlovka, *A. Ostenkov in 1882* (H, MW); Czernigov, Suraj, *M. G. Popov 933* (MW); Mimusinsk District, Kusehabar, *H. Printz in 1914* (LD); Voronezh, Graboberensko Experimental Station, *D. Raskatov in 1949* (MW); Khabarovsk Province, Troitskoye District, near Majak, *V. Sapegina 53* (MHA); Possiet District, S Ussuri Province, *A. P. Saverkina 590* (NY); Altai, Achelman R. valley, *B. Schischkin & P. Krylov in 1911* (NY, TUR); Primorski Province, near Ussuriysk, *A. Schreter in 1950* (DS); Khabarovsk Province, vicinity of Khabarovsk, *V. Shaga in 1959* (MHA), *V. Shaga 13* (MHA); Moscow Province, Naro-Tominsk, near Alabino, *A. K. Skvortsov 10237, 10238* (DS); Tula Province, Oka R. valley near Krassnoje, *A. K. Skvortsov in 1971* (MO); Primorski Province, Rikard Island, *A. K. Skvortsov in 1967* (MO); Primorski Province, at the Kedrovaya R., *G. Smirnova 2205* (DS); Bahilovska, Zhigulevsk Forest Reserve, *A. Uranov & I. Syryna 1577* (MW); Primorski Province, Khasan District, vicinity of Barabasch, *K. Vegener in 1964* (MHA); Primorski Province, near Vladivostok, *V. N. Voroshilov in 1958* (DS); Primorski Province, near Okeanskaya, *V. N. Voroshilov 4728, 4851, 4883, 9136* (MHA); Khabarovsk Province, Bogorodskaya District, near Tir, *14 August 1975* (MHA). SAKHALIN: near Kromogorsk, *A. Chernyayeva in 1961* (MHA); Vladimirov, *U. Faurie 422* (BM, KYO, P), *423* (BM, P); Moneron Island, *S. Komat in 1915* (TI); Galkinovlaskoe, *T. Miyake in 1906* (SAPA); E coast, Dubki, *T. Miyake in 1906* (SAPA); Kotan, Todomoshiri, *T. Miyake in 1906* (SAPA); Futarakipaachi, *G. Nakahara in*

1906 (TNS); Torepata, *G. Nakahara in 1906* (TI); Moneron Island, *Stepanova 231a* (MHA); Fukakusa, Kawagishi, *S. Sugawara in 1926* (SAPA); Fukakusa, *S. Sugawara 167* (SAPA).

ASIA

CHINA. HEILUNGKIANG: Harbin, *Jettmar in 1926* (W); Chi-hsi ("Tchi-sida-gou"), *V. Komarov in 1897* (P); near Shitokheza Station, *D. Litvinov 1968* (LE, NY); Sungari, Njelbu, *C. Maximowicz in 1859* (NY); at the Amur R., *N. M. Przewalski in 1867* (BM); I-ch'un Hsien, Wu-ying, *C. T. Tui et al. 7906* (PE). HOPEH: Peking, mountains, *A. David in 1862* (P); plains of Petcheli and mountains N of Peking, *A. David 438* (P); Hsiao-wu-tai-shan, Yang-kia-p'ing, Tang-lin, *H. Smith 230* (S, UPS); Cho-lu Hsien, Yang-chia-p'ing, Lao-po-ling, *C. K. Yang s.n.* (PE); Cho-lu Hsien, Yang-chia-p'ing, Tung kou, *C. K. Yang 606* (PE); Yung-ning, P'ai-t'a, *A418* (S); P'ai-t'a, Hsien-hwa, *H. Serre in 1930* (W); Ssu-t'a-kou, *in 1956* (PE 2150). KIRIN: Chang-wan, Ch'ai-lin-tun, *B. A. Ivashkevitch 487* (LE); Shen-yang to Chi-lin ("Mukden to Kirin"), Tang-ho-ko, *H. E. M. James in 1886* (K); Chang-pai-shan, and to Tang-ho-ko, Sungari R., *H. E. M. James in 1886* (K); O-mu-so, Palu-odi valley, *V. Komarov in 1896* (GH); O-mu-so, *V. Komarov in 1896* (K); O-mu Hsien, Tashantsuitzu, *H. W. Kung in 1931* (PE); Sung-hua-chiang ("Sungatschis"), *Maak s.n.* (K). LIAONING: Between the villages of Fu-eun and Dungan, *Y. L. Chang 56* (LE); Chi-kuan-shan, *M. Kitagawa in 1926* (TI) *and in 1931* (TI); Hoten, Renzankan, *I. Yamatsuta 951* (TNS). Shansi (Shantung?): Mt. Tai-shan, *T. Shinagawa 64* (TNS). SHANTUNG: 500 km S of Peking, *L. Chanet & J. H. Serre in 1903–1935* (P); top of Mt. T'ai-shan (PE 384243). PROVINCE UNKNOWN: Chi-kuan-shan, *M. Kitagawa in 1931* (TI); Kankyo-do, Tozan-rei, *K. Maeda in 1907* (TI); Kou-tou, *M. Takahashi 51* (TNS); Tsuka, *M. Takahashi 986* (TNS); Coast of Manchuria, 44°–45° N. Lat., *C. Wilford in 1859* (W).

JAPAN. HOKKAIDO: Abashiri-shicho, along the Okoppe-gawa R. at Sako-hashi Bridge, *D. E. Boufford & E. W. Wood 19799* (CM, K, KYO, MHA, MO); Okoppe-cho, 15.9 km NE of Nishiokoppe, *D. E. Boufford & E. W. Wood 19812* (CM, K, KYO, MHA, MO, NCU, PE); Abashiri-gun, Tsubetsu-cho, Lake Chimikeppu-ko, *D. E. Boufford 19781* (KYO, MO); *T. Matsuki in 1974* (MAK); Abashiri-gun, Memambetsu-machi, en route from Memambetsu to Yobita, *M. Wakabayashi et al. 246* (KYO). Hidaka Shicho, Shizunai-cho, 14 km ENE of Shizunai, *D. E. Boufford & E. W. Wood 19671* (KYO, MO); Samani-gun, Samani-cho, Okada, *D. E. Boufford & E. W. Wood 19689* (KYO, MHA, MO, NCU, PE). Iburi-shicho, Numanohata, *J. Hanzawa in 1899* (SAPA); Oshamanbe, *T. Kawakami in 1892* (SAPA); Toikambetsu, *T. Saito 91,19* (SAPA). Ishikari-shicho, Sapporo, Mt. Maru-yama, *M. Hara in 1942* (TI); Sapporo, *K. Miyabe in 1891* (PH), *Y. Tokubuchi in 1890* (MO, SAPA); Sapporo, Makomenai, *Tokuguchi in 1894* (SAPA); Sorachi, Sorachibuto, *K. Miyabe in 1891* (GH, KYO, SAPA, TI). Kawakami-shicho, Nakagawa-cho, hwy 40 just S of Nakagawa, *D. E. Boufford & E. W. Wood 19826* (MO). Kushiro-shicho, Shibecha-cho, 3.6 km S of Shibecha, *D. E. Boufford & E. W. Wood 19751* (MO); Kawakami-gun, Shibecha Experimental Forest of Kyoto University, *D. E. Boufford & E. W. Wood 19765* (BM, CM, E, G, K, KYO, MHA, MO, NCU, NY, P, PE, S, SHIN, TUS, UC); Shibecha forests, *U. Faurie 4930* (G, P); Shibecha-cho, in the vicinity of Shibecha Experimental Forest, *H. Koyama 1729* (MAK, KYO); Kushiro, Tomachise, *H. Hara et al. in 1974* (KYO, TI); Yukiuchi-mura, *W. (K)obana in 1895* (SAPA); Kamiaboro, *A. Umezawa in 1956* (SAPA); Akkeshi-gun, Aikeppu-misaki, *T. Nakashima in 1960* (KANA); Sonteki, *K. Miyabe in 1894* (SAPA). Nemuro-shicho, side of Lake Furen, *K. Ito in 1962* (SAPA). Shiribeshi-shicho, foot of Mt. Yotei-zan, beside L. Hangetsu, *M. Mizushima 2605* (TI); Yoichi, *I. Yamamoto 4979* (KYO). Tokachi-shicho, Urahoro-cho, 10.2 km W of Tokachikobetsu, *D. E. Boufford & E. W. Wood 19723* (BM, CM, E, G, K, KYO, MHA, MO, NCU, PE, UC); Aikoku, Obihiro-shi, *G. Murata 22035* (KYO); Urahoro, *H. Yokoyama 429* (SAPA); Ikera-cho, *H. Yokoyama 3173* (TI). SHICHO UNKNOWN: Oshima, Mena-kawa valley, *F. C. Greatrex 668* (SAPA); Asajino, *S. Watanabe in 1954* (SAPA); Lake Shibunai, *T. Sakuma in 1953* (SAPA); Kusuri, *K. Miyabe in 1884* (SAPA, TI); Rishiri Island, *S. Hori in 1887* (SAPA). HONSHU: Tochigi Prefecture, Nikko, *H. Ito 310* (TI).

KOREA, NORTH. Ouon-san, *U. Faurie 283* (K, P); Kan-nan, Senbutsu-san, *M. Honda 39* (TI); San-su, Yellow R., San-kori-muri, *V. Komarov in 1897* (LD); Kei-gyo, Kankyo-hoku-do, *M. S. Hi 958* (KYO); Kongo-san, Makkiri, *T. Nakai 5682* (TI); Koryu-do, Hokueibo, *T. Nakai et al. in 1933* (TI); Kankyo-hoku-do, Kisshu-gun, Eikodo, *J. Ohwi in 1930* (TNS); Eikodo, Reketsui R., *J. Ohwi 3065* (KYO); Mt. Kongo-san, *S. Okuyama in 1940* (TNS); Kankyo-hoku-do, Ranan, *T. Saito 1614* (KYO); Kankyo-hoku-do, Modzan, *T. Saito 2731* (KYO); Mt. Kogen-san, Kogen-do, *T. Uchiyama in 1902* (TI); Kankyo-hoku-do, Kainei, *K. Yoshinaga in 1934* (TNS); Kamkyong-puk-do, *10382* (MICH); Kakyo-do, Nanyo village, *no further data* (KYO).

KOREA, SOUTH. Kogen-do, Somoku-do, *T. Uchiyama in 1902* (TI).

KOREA, LOCALITIES UNKNOWN. Shosen-ri, San-zi, *T. Nakai 3678* (SAPA); Sanyo-eguchi, *T. Nakai 3543* (TI).

As mentioned above, *Circaea lutetiana* subsp. *quadrisulcata* is most similar to subsp. *canadensis* but differs from that subspecies in lacking a bracteole at the base of each pedicel. *Circaea mollis* is most similar to *C. lutetiana* subsp. *quadrisulcata* in eastern Asia but has the stem usually densely pubescent, smaller flowers, shorter pedicels, and abundant racemes at the apex of the stem and at the tips of many of the upper, axillary branches. In addition, the petals in *C. mollis* are always white and the sepals are always green. The leaf bases in *C. mollis* are cuneate and rarely almost rounded.

The ranges of *Circaea lutetiana* subsp. *lutetiana* and subsp. *quadrisulcata* overlap in the vicinity of Moscow and in the eastern part of the European Soviet Union but most specimens from that area can be attributed to one or the other subspecies without a great deal of difficulty, especially when mature fruits are available. Further field work in this area of overlap should be carried out to determine the amount of intergradation that occurs in the two subspecies.

A single specimen of Polatschek (in 1973, W) from the lower Isel Valley of Austria between Lienz and Tratte, is puzzling in that it is unmistakably *Circaea lutetiana* subsp. *quadrisulcata*. Whether this collection represents a recent introduction, the extent of possible variation in the European *C. lutetiana*, or a previously unknown, disjunct population is uncertain. Field work by persons in a position to do so should be undertaken to determine the nature of this population.

H. Léveillé (1912) listed two names under *Circaea mollis* Sieb. & Zucc. var. *maximowiczii* H. Lév., "pogogyna" and "pachystyla," that need clarification. Based on Léveillé's consistent use of the terms forme, var., etc. to precede names that he wanted to recognize formally, it does not appear to be his intent to assign any particular taxonomic rank to these two names but only to point them out as "lusi" (sports, variants) of var. *maximowiczii*, as he similarly did under *C. lutetiana* with "albiflora," "rubriflora," "cordifolia," etc., even though in his preceding sentence he states "One can distinguish the following two forms:" (trans. from French).

4c. **Circaea lutetiana** L. subsp. **lutetiana**—FIG. 12.

Circaea major Lam., Fl. Fr. 3: 473. 1778. Nom. subs., *C. lutetiana* L. in syn.

Circaea vulgaris Moench, Meth. 279. 1794. TYPE: Germany, "frequens an der Schneisse prope Giesselberg." According to Ascherson and Magnus (1870), Moench's herbarium was ". . . just recently lost through the lamentable carelessness of the owner, . . .").

Circaea nemoralis Salisb., Prod. 276. 1796. Nom. subs., *C. lutetiana* L. in syn.

Circaea racemosa Hull, Br. Fl. 6. 1799, pro parte. Nom. subs., *C. lutetiana* L. and *C. alpina* L. in syn.

Circaea racemosa Hull var. *lutetiana* (L.) Hull, Br. Fl. 6. 1799.

Circaea pubescens Pohl, Tentamen Fl. Bohemiae 1: 6. 1809. Nom. subs., *C. lutetiana* L. in syn.

Circaea ovalifolia Stokes, Bot. Mat. Med. 1: 26. 1812. Nom. subs., *C. lutetiana* L. in syn.

Circaea lutetiana L. forma *ovatifolia* Lasch, Linnaea 2: 446. 1827. TYPE: E. Germany, Neumark.

Circaea lutetiana L. forma *cordifolia* Lasch, Linnaea 2: 446. 1827. TYPE: E. Germany, Neumark.

Circaea lutetiana L. forma *glaberrima* Lasch, Linnaea 2: 446. 1827. TYPE: E. Germany, Neumark.

Circaea lutetiana L. var. *cordifolia* G. Meyer, Chl. Hanover 100. 1836. TYPE: only locality given by Meyer for this variety is "im Herrenhauser Park" (GOET, a specimen labelled by G. F. W. Meyer as type).

Circaea lutetiana L. *β glabra* Petermann, Fl. Lips. Excurs. 28. 1838. The herbarium at Leipzig, where Petermann's specimens were probably deposited, was destroyed during World War II.

Ocimastrum verrucarium (Gesner & Bauhin) Rupr., Fl. Ingr. 368. 1860. Nom. subs., *C. lutetiana* L. in syn.

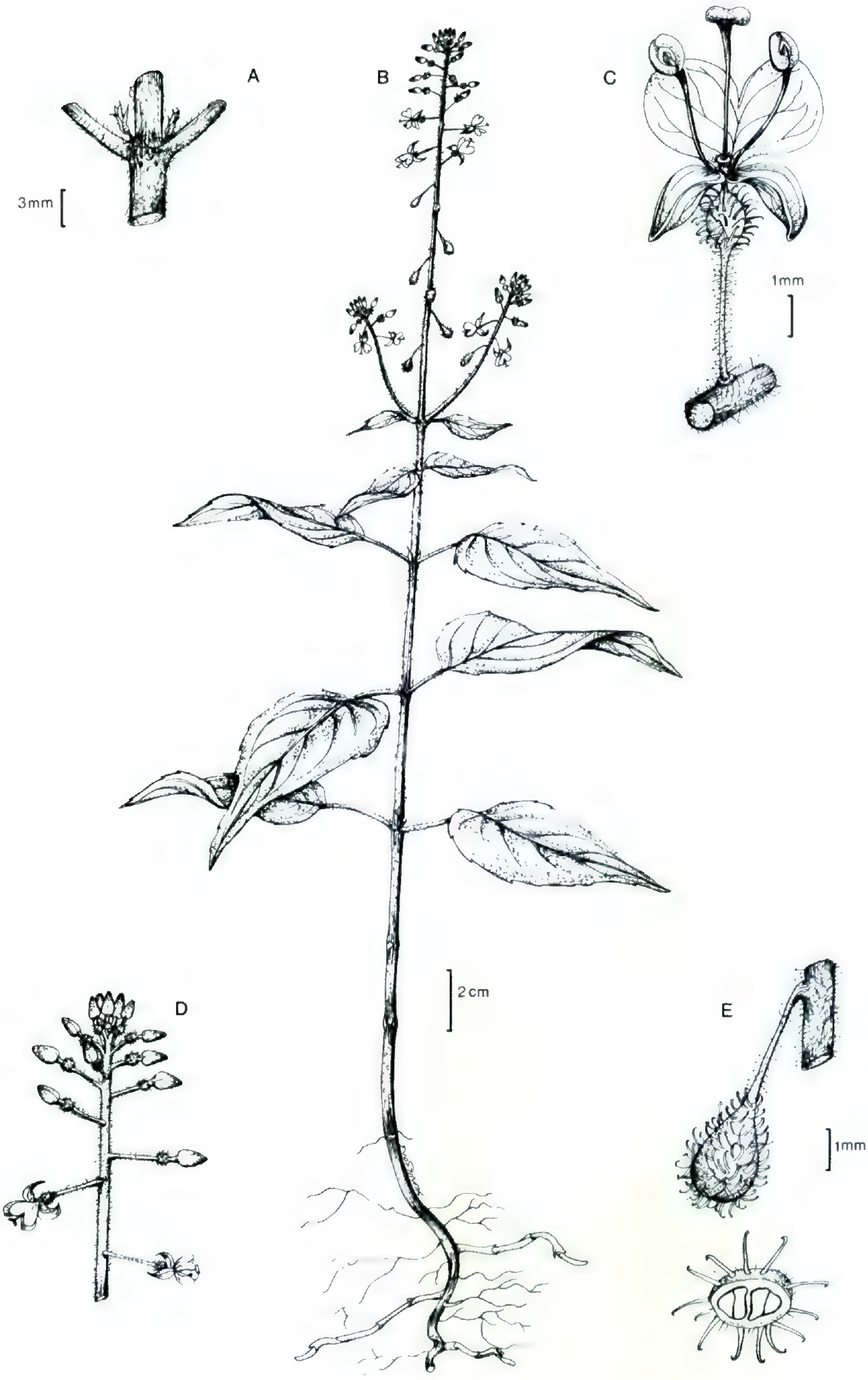


FIGURE 12. *Circaea lutetiana* L. subsp. *lutetiana*.—A. Node of upper stem.—B. Habit.—C. Flower with petal removed; note exserted nectary.—D. Inflorescence.—E. Fruit. From *Skvortsov s.n.* (MO 2352081).

Circaea lutetiana L. var. *obscurata* Grognot, Carian Cat. Pl. Saone-et-Loire 153. 1863. TYPE: France, moist mountain forests between St. Prix and Goulette, and towards Crot-Maxin R. (AUT, lectotype).
Circaea lutetiana L. var. *atrosanguinea* F. Schultz, Pollichia 20: 144. 1863. TYPE: Germany, on the porphyry of Yburg near Baden.
Circaea lutetiana L. var. *decipiens* Asch., Fl. Prov. Brandenburg 2: 214. 1864. TYPE: Not located.
Regmus lutetianus (L.) Dulac, Fl. Hautes Pyr. 328. 1867. Nom. illegit.
Circaea lutetiana L. var. *erythrocalyx* O. Kuntze, Taschen Fl. Leipzig 257. 1867. TYPE: E. Germany, in forest before Leutzsch. Kuntze's collections were at Leipzig, which was destroyed during World War II.
Circaea lutetiana L. subsp. *mediterranea* Asch. & Magnus, Bot. Zeitung (Berlin) 28: 783. 1870. TYPE: Not located.
Circaea lutetiana L. var. *glaberrima* (Lasch) Asch. & Magnus, Bot. Zeitung (Berlin) 28: 780. 1870.
Circaea lutetiana L. var. *brevipes* Battand., in Battandier and Trabut Fl. Alg. (Dicotyl.) 317. 1889. TYPE: Algeria, stream of Singes, Djurdjura.
Circaea lutetiana L. var. *longipes* Battand., in Battandier and Trabut Fl. Alg. (Dicotyl.) 317. 1889. TYPE: Algeria.
Circaea lutetiana L. var. *ovatifolia* (Lasch) Beck, Fl. Nieder-Oster. 2: 695. 1892.
Circaea lutetiana L. var. *cordifolia* (Lasch) Beck, Fl. Nieder-Oster. 2: 695. 1892. non G. F. W. Meyer, 1836.
Circaea lutetiana L. var. *villosa* Beck, Fl. Nieder-Oster. 2: 695. 1892. TYPE: Austria, on the Thalhofriese of the Schneebergs.
Carlostephania major (Lam.) Bubani, Fl. Pyrenaea 2: 659. 1900. Nom. illegit.
Circaea lutetiana L. forma *mediterranea* (Asch. & Magnus) Paol., in Fiori & Paoletti, Fl. Anal. It. 2: 135. 1900.
Circaea lutetiana L. var. *hirsuta* Podp., Verh. Zool. Bot. Ges. Wien 52: 650. 1902. TYPE: "Cepelare in den Rhodopen."
Circaea lutetiana L. forma *pseudo-cordata* H. Lév., Bull. Acad. Int. Géogr. Bot. 22: 218. 1912. No specimens cited.
Circaea lutetiana L. forma *hirtopetiolata* H. Lév., Bull. Acad. Int. Géogr. Bot. 22: 218. 1912. No specimens cited.
Circaea lutetiana L. forma *brevipes* (Battand.) H. Lév., Bull. Acad. Int. Géogr. Bot. 22: 218. 1912.
Circaea lutetiana L. var. *typica* Fiori, Nuov. Fl. Anal. It. 2: 15. 1925.
Circaea lutetiana L. forma *aprica* H. Lév. ex Hegi, Ill. Fl. Mit.-Eur. 5: 877. 1925.
Circaea lutetiana L. forma *albiflora* H. Lév. ex Hegi, Ill. Fl. Mit.-Eur. 5: 878. 1925.
Circaea lutetiana L. forma *longipetiolata* H. Lév. ex Hegi, Ill. Fl. Mit.-Eur. 5: 877. 1925.
Circaea lutetiana L. forma *rubriflora* H. Lév. ex Hegi, Ill. Fl. Mit.-Eur. 5: 878. 1925.
Circaea lutetiana L. forma *truncata* H. Lév. ex Hegi, Ill. Fl. Mit.-Eur. 5: 877. 1925.
Circaea lutetiana L. forma *umbrosa* H. Lév. ex Hegi, Ill. Fl. Mit.-Eur. 5: 877. 1925.
Circaea lutetiana L. forma *carneostyla* H. Lév. ex Hegi, Ill. Fl. Mit.-Eur. 5: 878. 1925.
Circaea lutetiana L. subvar. *cordifolia* (Lasch) Hayek, Prod. Fl. Balk. Pen. 1: 949. 1926.
Circaea lutetiana L. forma *hirsuta* (Podpera) Hayek, Prod. Fl. Balk. Pen. 1: 949. 1926.

Plants 1.5–9 dm tall, densely to sparsely pubescent, rarely the stem subglabrous; the stem with soft, falcately recurved hairs ca. 0.2 mm long, sometimes with capitate and clavate-tipped hairs ca. 0.4 mm long and soft, sharp-pointed, straight or slightly curved, patent hairs intermixed; the petioles with hairs as on the stem but the falcate hairs upwardly curved; the leaves glabrous or, more commonly, pubescent, especially near the base and along the main veins on the lower, and occasionally also on the upper surface, with soft, falcate hairs and occasionally also with long, straight hairs ca. 1 mm long if these present on the stem, interveinal areas less densely or scarcely pubescent; leaf margins with short falcate cilia and with long straight hairs if these present on the stem. Leaves (3–)6–11(–15) cm long, (2–)3–5.5(–12) cm wide, very broadly elliptic to deltoid ovate but most commonly ovate to lanceolate ovate. Petioles densely to sparsely pubescent, with upwardly curved, falcate hairs ca. 0.2 mm long, sometimes with longer, straight or slightly curved hairs, 0.5–0.8 mm long, intermixed if these present on the stem. Flowering pedicels (2–)3–5.2(–9) mm long, without, very

rarely with, a minute setaceous bracteole at the base. Fruiting pedicels 3.8–6 (–10) mm long. Buds (2.4–)3.2–4.5(–5.4) mm long, 1–1.9 mm thick just prior to anthesis. Floral tube (0.8–)1.1–1.8(–2.4) mm long, linear obtriangular to slender funnelform in outline. Sepals oblong to ovate, (1.6–)2.5–3.5(–4.5) mm long, (0.8–) 1.2–2 mm wide. Petals (1.4–)2–3.7 mm long, (1.8–)2.3–3.4(–4) mm wide, white or pink; the apical notch (0.6–)1.6–2(–2.4) mm deep, ½ to slightly over ½ the length of the petal. Filaments 2.5–3.5(–4.3) mm long; anthers 0.6–0.8(–1) mm long, 0.3–0.6(–0.9) mm thick. Style 3.3–4.5(–6) mm long; stigma 0.2–0.4(–0.6) mm tall, 0.4–0.9 mm thick. Nectar secreting disc 0.2–0.6 mm tall, 0.3–0.5(–0.9) mm thick. Mature fruit 2.8–3.3(–3.8) mm long, 1.4–2(–2.4) mm thick, clavate to obovate, rounded at the apex, tapering smoothly to the pedicel, without prominent ribs and sulci. Fruiting pedicels reflexed, often sharply so. Combined length of pedicel and mature fruit (6.3–)8–11(–15) mm long. Gametic chromosome number, $n = 11$.

LECTOTYPE: Sheet 25-1 (LINN) "lutetiana 1," presumably from southern Sweden, can be considered as the lectotype; Linnaeus (1753) wrote the diagnosis for *Species Plantarum,* and doubtless knew the species well.

Distribution (Fig. 13): Moist, temperate deciduous forests, commonly with *Fagus, Carpinus,* and *Alnus*. Southern Scandinavia south to the mountains of northeast Africa, along the north side of the Mediterranean Sea and eastward to northeastern Iran, from the Caucasus Mountains to southwestern U.S.S.R. and through Poland to the Baltic Sea, scattered eastward to the vicinity of Moscow. From sea level to ca. 2,200 m. Flowering, June through August.

Representative specimens examined:

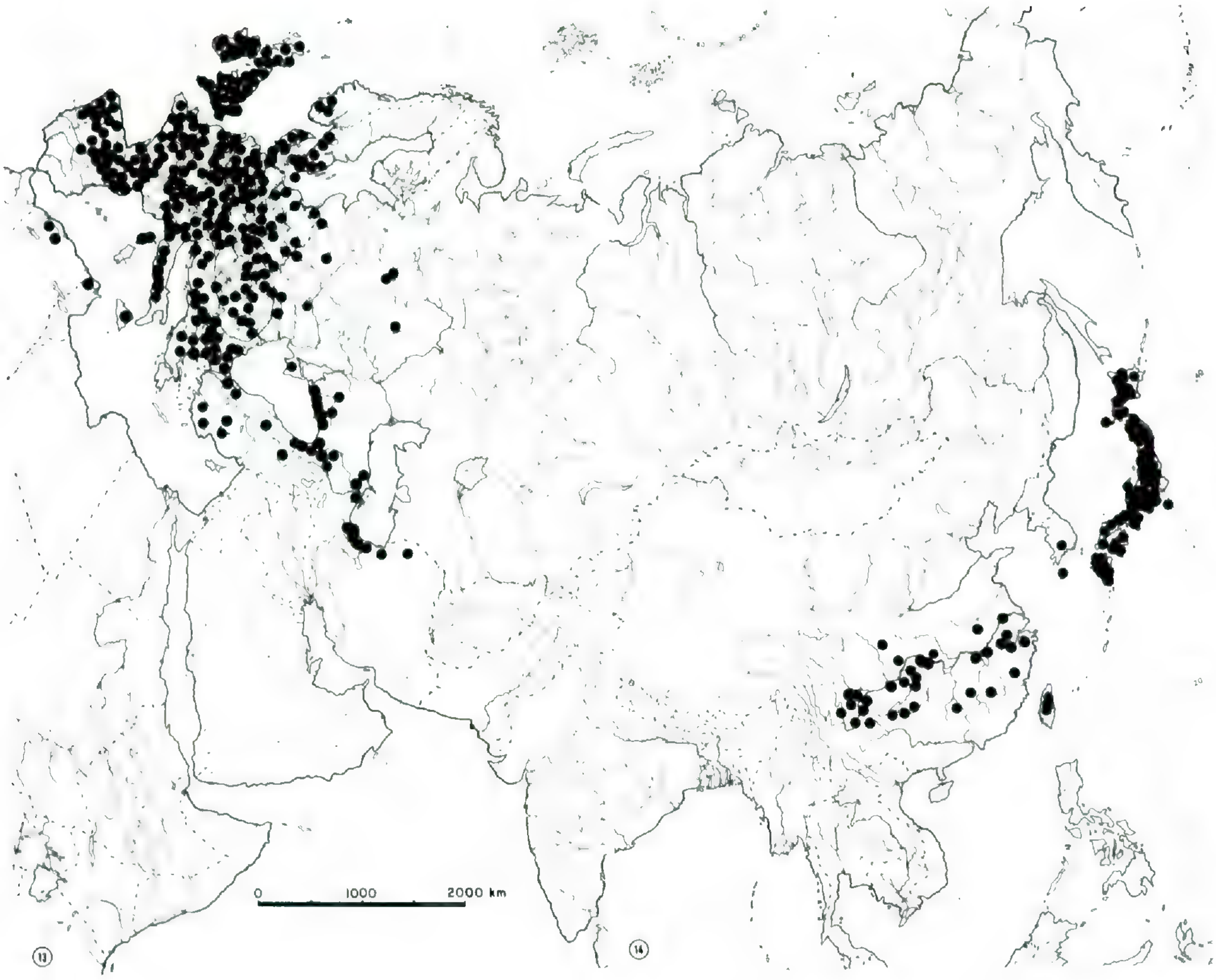
EUROPE

ALBANIA. Klementi, *A. Balacci 219* (G, W).

AUSTRIA. Mur R. ca. 1 km E of Peggau, *R. Alava & H. Teppner 2950* (TUR); Marchau, Marchegg, *Drescher in 1971* (W); Vienna, *Heimerl in 1923* (OKL, WTU); Schwertberg, *Keck s.n.* (UC); Aistersheim, *Keck s.n.* (ISC, MO, POM, UC, W); Salzburg, Etenan, *E. Korb in 1924* (W); Salzburg, in the vicinity of the salt works, *E. Kreiamitz in 1845* (UC); Vorarlberg, Jagdberg near Schlins, *A. Neumann in 1967* (W); Vorarlberg, Bocksberg near Neuburg, *A. Neumann in 1967* (W); Arnoldstein, *A. Palmer in 1870* (H); N Weisskirchen, Ohrensdorf, *F. Petrolz 835* (SUM); Tyrol, Thal, *T. Pichler in 1896* (US); Kärnten, Becken, S of Klagenfurt, *Pokorny in 1920* (W); Vorarlberg, Feldkirch, *A. Polatschek in 1968* (W); Vorarlberg, Rheingau, Bregenz, *A. Polatschek in 1971* (W); Nordtirol, Oberinntal, *A. Polatschek in 1972* (W); Steiermark, near Deutschlandsberg, *E. Preissmann in 1867* (W); Steiermark, near Mixnitz, *E. Preissmann in 1895* (W); Vorarlberg, Bregenzerwald, Pfänder-Gebiet, Gebhartsberg, *R. Seipka in 1971* (W); SE Steiermark, near the Schlossmeirei, *R. Seipka in 1970* (W); Steiermark ("Stiria media"), Stainzerbach R. near Stainz, *P. v. Troyer, Fl. Stir. Exs. 644* (DS, H, ND, UC, W); Steiermark ("Stiria superior"), Gröbming, *E. Wibiral, Fl. Stir. Exs. 643* (H, ND, W); Dornbach, Vindobonen, *Woloszczak, Fl. Exs. Aust.-Hung. 1274* (B, H, L, MIN, US, W).

BELGIUM. Liege, Vierset-Barse, *P. Auquier 3161* (H, TUR); Henri Chapelle, *E. Bodart in 1913* (WTU); Heysel, forests in vicinity of Hosseghem, *M. Gams in 1924* (UC); Beaumont, *A. Hardy 278* (MT); Meise, Bouchont, *A. Lonobrie 12542* (PH); Theux, *M. Mairlot in 1904* (MO); Pirengen, Colmont, *Michiels in 1931* (MT); Anlier, *Wilezele 793* (MO); Vertrijk, *A. Thielens in 1863* (R).

BULGARIA. Varna, *L. Brumll in 1886* (B); Sofia region, *N. Nikolov 853* (G, H, MA, UBC, W, WU); near Karlova, *N. Vihodcevsky in 1968* (GOET); Pieniawka, Momina Klisura, *T. Wisniewski & H. Slivinska in 1927* (WA); Gorna Ljubata, Kjustendil Dist., (SOM 54479)*; Vibosha Mt., (SOM 54459); near Teteveni, (SOM 54477); Gradishte near Gabrovo, (SOM 54473); Borushtica, Stara Zagora Dist., (SOM 54474); Karash, Lukovit Dist., (SOM 54475); Balkan Mt., Bertemeto, (SOM 129063); Rodopy Mts., near Bachkovo, (SOM 54464); Balkan foothill Mts., Zlabaritza Veliko Tarnovo Dist.,



FIGURES 13–14.—13. Distribution of *Circaea lutetiana*. L. subsp. *lutetiana*.—14. Distribution of *Circaea erubescens* Franch. & Sav.

(SOM 54458); Ljubin Mt., near the monastery, (SOM 130262); Strandza Mt., near Gramatikova, (SOM 43597). * Data for specimens in SOM were supplied by Mincho Anchev.

CZECHOSLOVAKIA. Brno, near Komarov, *O. Mrkos 351* (CAS, DAO, H, KRA, MT, POM, TUR, W, WA); Malinec, *Priluitz in 1868* (US); E Moravia, Novy Hrozenkov near Vsetin, in the Skalici valley, *G. Rican 1149* (DAO, DS, H, KRA, MO, MT, POM, TUR, UC, W, WA).

DENMARK. Charlotenland, *G. Bagenholm in 1893* (MIN); Själland, Skodsborg, *U. Bailund in 1929* (H); Island of Möen, *J. Ball in 1888* (IA); Hammerbakker, dist. 4, *L. Br. Holm-Nielsen in 1966* (MO); Hanstedskov, dist. 24, *L. Br. Holm-Nielsen in 1966* (MO); Tarbaek, *H. Gravers in 1887* (H); Tåsinge Island between Fyn & Langeland, *K. U. Kramer 5829* (NCU); Jutland, Lisbjerg, N of Aarhus, *K. Larsen 155* (COLO, DS, H, MA, SMU, US, W, WTU); Ermelunden, Gentosste, *K. Larsen in 1956* (H, SMU); Sjaelland, Vesterskov woods near Furesø, N of Copenhagen, *T. Leth in 1861* (DS); Sjaelland, Fredensborg, *H. Muchardt in 1915* (RSA); Lolland, dist. 36, Nysted landsogn, Roden Skov, *C. M. Normann in 1959* (DAO, MT, RM); Bornholm, Åkirkeby, *H. Roivainen in 1977* (H); Kööpenhamina, Uesterbrohaue, *H. Såltin in 1961* (TUR); Sjalland, Vordingborg, Rosenfelt, *T. Sundin in 1964* (CAS); Jylland, Horsens, *J. Suominen in 1965* (H); Zealand, S of Haraldsted Sø, Ringsted, *J. Svendsen 62* (COLO, H, MO, NCU, OMA, PH, TUR, UBC, W); Själland, Lyngby, *L. Tiensuu in 1950* (H); Svendborg, Fyen, *without collector in 1869* (MT).

FRANCE. Aisne, Villers, Cotterets, *C. d'Alleizette 951* (K, RSA); near Sarrebourg, *Baudot in 1868* (POM, mixed sheet, with *C.* × *intermedia*); Gannat, *P. Billiet 929* (MT); Servoz, Alta Sabaudia, *Bouchard in 1910* (MO); Deaux-Sevres, near Lezay, *E. Contre in 1959* (CAS, DAO); Aisne, central Jura, Bas-Bugey, St. Boys, *H. Coste & Brunard 2087* (MT); Gironde, La Brede, Chateau, *H. Coste et al. 1282* (MT); Beziers, *Daenen in 1855* (G); Compiegne, *F. Debray 1996* (UC); Dauphine, St. Marrellin, *Delannay in 1891* (W); Argeles, *B. Delessert in 1894* (G); Baugy, *P. Eveque in 1898* (H);

St. Georges d'Espiranches, *G. Gavelle in 1968* (CAS); Savoie, Mt. Mirz, *Geneva in 1825* (US); Gap au Chauret, Alps, *Girod in 1904* (G); Corsica, Lopigna, Cruzzini R., *H. v. Hattum 5626* (L); Bretagne, Quimper, *Hodgdon & Hodgdon 16443* (NHA); Mauleon-Soule, Haies, *J. Jallu 1223* (RO); near Paris, *E. Jeanpert in 1890* (MIN); Lyon, *Herb. Jordan in 1853* (W); Brittany, near Huelgoat, *S. L. Jury 417* (RNG); Corsica, Bastia, *L. Kralik in 1849* (G); Nierve, Dornes, *S. Lassimonne 66* (US); Normandy, Montmiral, *A.-L. Latacq in 1908* (COLO); Aude, Bassin de St. Ferreol, *J. C. v. Loon 414* (NCU); Jersey Island, St. Sauveur-de-Jersey, *Louis-Arsene 4098* (DAO); Creuse, St. Avit-de-Tardes, *R. Lugagne 2981* (DAO, H, SMU, TEX), *R. Lugagne 6680* (LD, TUR); Pringy, *Luget in 1867* (MO); Teine et Oise, Mendon, *Mouillefarine in 1882* (CM); Boubonne les Bains, Mt. Marne, *Mouillefarine in 1888* (UMO); Versailles, *K. L. Oesch in 1924* (TUR); Bretagne, St. Lunaire, *B. Ohovi in 1949* (H); Paris, *Parmentier circa 1812* (PH); Nantes, Seminary Property, *Br. J. Peter in 1908* (DAO); Corsica, Corti, *Pittone s.n.* (W); Corsica, Cargiaca, *A. Renvall in 1905* (H); Eclaron, *B. de Retz in 1933* (WTU); Corsica, Evisa, *E. Reverchon 423* (DS, G, K, MA); Vaucresson, *W. Schoenefeld in 1843* (H); Versailles, *I. Tidestrom 12317* (NA); above Rouen, Mt. St. Aignan, *I. Tidestrom 12970* (US); Hautot, St. Sulpice, *I. Tidestrom 13875* (POM, US); vicinity of Paris, *G. B. Wakeman s.n.* (CM); Chaiville, Veligy, *without collector in 1908* (H).

GERMANY, EAST. Leipzig, *A. H. R. Buller in 1898* (WIN); Lobau, *G. Cufodontis in 1925* (W); Magdeburg, *H. Eggert in 1866, 1867* (MO); Leipzig, *G. Fischer in 1895* (SMU); near Potsdam, *Joachin s.n.* (H); Büchenwaldern near Kalksburg, *E. Korb in 1918* (W); Erzgebirge, from Doppelburg *via* Eichwalds to Fuchsbutteljagdhaus, *E. Korb in 1925* (W); Leutzsch, *O. Kunze in 1862* (US); Kaltern, *P. Morandeff s.n.* (W); Dresden, *Reichenbach s.n.* (PH); Thüringen, *E. M. Reineck in 1900* (MIN); Mecklenburg, Parchim, *H. Roos in 1904* (H): Tharandt, *R. Sarvas in 1920* (H); near Stöcker, *F. Schwarzl in 1871* (W); around Wiesenränder, W of Gleichenberger-burg, *R. Seipka in 1970* (W); Alta Statberg, *Vock in 1882* (MSTR, US); Karlmarxstadt (Chemnitz), *M. Weicker in 1829* (W).

GERMANY, WEST. Erlangen, *M. Beiapts in 1861* (MO); Upper Hessen, *O. Degener 23399* (SMU); near Monkenbursch, Menningshausen, *Dubruck 2290* (MSTR); Hannover, *Erhart 121* (W); near Oberaudorf and Fischbach, *G. Eigner in 1903* (UC, WA); Frankfurt, *G. Engelmann in 1820* (MO); Holstein, Ostsee coast, *Girtf? in 1935* (W); Heidelberg and vicinity, *Girtf? in 1935* (W); Hessen, Starkenburg, *Girtf? in 1928* (W); Hessen, Rheinhessen, *Girtf? in 1915* (W); Holstein, Lübeck, *Girtf? in 1938* (W); near München, *H. Glück in 1906* (W); Hohenstadt, *T. Hruby in 1933* (H); Oberhessen, Kreis Alsfeld, Gr. Felda, *H. Hupke in 1958* (OKLA, SMU); Kreis Alsfeld, Liederbach an Waldwegen, *H. Hupke in 1964* (SMU, VDB); Kreis Alsfeld, Weidenberg, *H. Hupke in 1965* (UT); Kreis Alsfeld, Koppenberg, *H. Hupke in 1967* (MONTU); Kreis Alsfeld, Liederbacher Teich, *H. Hupke in 1969* (SASK, USAS); Schleswig-Holstein, Siebenbaumen between Bad Oldesloe and Ratzeburg, *S. Jeppesen & K. Larsen, Fl. Germ. Exs. 30* (COLO, DS, GOET, H, MA, SMU, TUR, W, WTU); Emmendingen, Nimburg, *V. Kap 128* (W); between Oberstem and Wildenburg, *C. Knabe in 1905* (H); Aachen, *P. Krabler in 1857* (W); Botenwald, Mähren-Odertal, *K. Krischke in 1926* (B); Würtemberg, Rossberg, *B. Lindberg in 1891* (H); Isarthal near Grosshesselohe, *C. J. Mayer in 1902* (UC); Holstein, Lockstedter Lager, *L. Oesch in 1915* (H); Baden-Würtemberg, Stuttgart-Vaihingen, S of Kurmärkerster, *J. Penalosa 2903* (CAS); Westfalen, Meinberg, *Prager s.n.* (CAS); Berner Alps, *P. Reinsch s.n.* (OS); Kaiserstuhl, Schelingen near Breisach, *Stud. Biol. Rheno-Trai. 61-1936* (NCU); Sud-Niedersachsen, near Othfressen, *I. & H. Scholz 70216* (NCU); Hessen-Nassau, near Bassel, *Schulz in 1906* (B); Hamburg, *Steetz s.n.* (PH); E of München, S of Rosenheim, *P. Votila 20890* (H); Schleswig-Holstein, near Niendorf, *G. Wagenitz 454* (B); Oberhayn near Warstein, *Herb. Wiemeyer in 1917* (MSTR); Ruckeburg, *Wze in 1926* (MSTR); Minden, *Wze in 1926* (MSTR).

GREECE. Thassalia, Mt. Telio, *T. Aphentubis in 1887* (WU); Mt. Athos, *N. Ballalas in 1921* (US); Ipiros, Ionnina, Vikos Gorge below Kapesovo, *C. N. Goulimis 15181* (ATH); E Macedonia, Sidironezi-Skaloti, *C. N. Goulimis 15178* (ATH); E Macedonia, Halkidiki, Mt. Ayion-Ozos (Mt. Atkos), *C. N. Goulimis 15177, 15180* (ATH); E Macedonia, Boz-Dag, Ajios Petros-Mili, *C. N. Goulimis 15179* (ATH); Athos Pen., Moni Thilotheon, *C. N. Goulimis in 1947* (K); Thessalia, Agrafa, Mt. Pindo, *T. Heldreich in 1885* (WU); Volos, Zagora, *Raus 949* (ATH); Thasos, 4 km SSW of Thasos, *S. Snogerup in 1971* (LD); W Macedonia, Pella, Almopia Dist., Platza, *E. Stamatiadou 19472* (ATH).

HUNGARY. Felsö Mocsolad, *L. Bano in 1946* (DAO); Debrecen, Hajdu, *R. Rapaics, Fl. Hung. Exs. 762* (DAO, H, MO, TUR, UC, W, WU); Carpathian Mts., Lct. Georgen, *A. Zahlbruckner in 1884* (W).

ITALY. Certosa di Pesio, *J. Ball in 1887* (CAS); near Bagni di Lucca, *J. Ball in 1844* (PH); Grappa, Mt. Bassanensium, *J. Ball in 1858* (MO); Piedmont, Luserna valley, *J. Ball in 1860* (MTMG); Rome, Latium, Paliano, *A. Beguinot 896* (K, NEB, RO, WU); Apennine Mts., *P. Bubani in 1804* (NMC); Rome, *A. Cacciato in 1954* (SMU); Genova, *Canepa in 1885* (RO), *R. Canneva in 1907* (H); Liguria, Polcavera valley, *R. Canneva in 1907* (RO); Bergamasques, Lake Rocco, *P. Chenevard in 1912* (G);

Bergamasques, Malgina valley, *P. Chenevard in 1913* (G); Sicily, Tortorici, *Citarda 726* (CM, PENN, RO); Toscana, Pracchia, *A. Contardo in 1953* (SMU); Albano, *F. Cortesi in 1880* (RO); Trieste, Rojano, *V. Engelhardt in 1884* (L); Scalenghe, *P. Fontana in 1924* (DAO); Bagni di Lucca, *O. Grampini in 1901* (RO); Neapolitani, St. Rocco R. valley, *Heldreich 51* (W); Napoli, *D. Hildreith in 1840* (G); Trieste, *Lani in 1952* (RO); Castagneta, *G. Lunne in 1957* (RO); Casalta, *A. Nabelli in 1886* (RO); Venaria Reale, Torino, *E. R. Paoletti in 1903* (NEB); Campagnano, *A. Pappi in 1900* (RO); Sicily?, Tusa, *Parlatore in 1877* (WU); Matese, *N. A. Pedicino in 1876* (RO); near Rome, *A. Pelosi in 1887* (PENN); S Michele in Teverina, *A. Poppi in 1900* (RO); Toscana, Massa, Resceto, *A. Ranhala in 1964* (H); Cottian Alps, *E. Rostan in 1880* (L); Tuscany, *D. Salla in 1890* (L); Massa, Rocca, *Wellegrini in 1940* (H); Friuli, *G. Zamburlini s.n.* (RO); Sicily, Caronia, *without collector in 1850* (G); Mt. Elmo, *without collector & date* (W).

LUXEMBOURG. Diekirch, *Denonville in 1952* (W).

NETHERLANDS. Utrecht, *C. C. Berg et al. 1000* (H, MA, MT, NCU, NO, TUR, UC, WTU); near Utrecht, forest of Oud-Amelisweerd, *H. F. J. v.d. Brugge in 1950* (MO, SMU, US); Domburg, *J. Burger in 1947* (MT); Utrecht, *F. Hartsen in 1860* (W); Oldenzaal, *L. G. Kop in 1948* (UC); Overijsel, Schijvenerveld near Delden, *P. v. Royen in 1948* (TEX); Wageningen, *K, d. Vries in 1948* (UC).

NORWAY. Hordaland, Skånevik, T. Braarud in 1927 (H); Midthordland, Hatviken, *R. Fridtz 24940* (H); Hordaland, Skånevik, Fjaere, *I. Jørstad in 1913* (SASK); Hordaland, Vangdalsberget, *S. K. Selland in 1915* (MT); Hordaland, Kvinnherad hd., *S. K. Selland in 1912* (COLO).

POLAND. Gdansk, Elblag (Danzig, Elbing), *C. Baenitz in 1881* (MSTR, W); Wroclaw (Breslau), between Oberglauche and Skarsine, *C. Baenitz in 1898* (B, US, W); Pommerana, Kolobrzeg (Kolbergmünde), *C. Baenitz in 1881* (MSTR); Tomaszow, *F. Blonski in 1890* (WA); Brenna Leinica–Beskid Slaski, *M. Broda in 1968* (KRA); Brenna Holcyna–Beskid Slasky, *M. Broda in 1967* (KRA); Vilpotny, Pornachowice Dolne, Myslenichi, *V. T. Dobranske in 1925* (KRA); Gostynski, Konstantynow, *K. Drymmer in 1895* (WA); Gostynin Dist., Sanniki, *K. Drymmer 628* (W, WA, WU); Silesia, Slask Dolny, Wzgorze Joanny K. Milicza, *S. Golowin 41* (DAO, H, SMU, TUR, WA); Nowy Sacz Dist., Lomnica Zdroj., *K. Grodzinska in 1957* (MO, US); Dobrzynska, *A. Halewski in 1890* (WA); Wroclaw (Breslau), *G. Hieronymus in 1890* (WA); Premyslany, Podalia, *Kostrakiewicz in 1930* (POM, US); Carpatian Mts., Mt. Beskid Niski, *I. Kucowa & H. Piekos 137* (COLO, H, KRA, MO, NCU, PH, SMU, UBC, UC, WA, W); Dubie-Dolina Racławki, *M. Mazaraki in 1948* (KRA); Stanowisko, Cienisty las, Myslenice, *K. Potyra in 1959* (KRA); Jorfowisko, Gryfice, *K. Poulikouska in 1950* (WA); Dublanach, *M. Raciborski 150* (L, W); Jura, Krak-Wielunska, *Z. Radwanska s.n.* (WA); Gorce–Rezerwat Orkana, *St. Pelc in 1954* (KRA); Beskid Niski, Cergowa Gora, *T. Tauk in 1955* (KRA); Wadowice Dist., Kalwaria Zebrzydowska, *J. Trela, Pl. Exs. Pol. 349* (L, MT, WA); Wadowice Dist., Lanckorona, *J. Trela, Pl. Exs. Pol. 349* (DS, L, MO, MT, WA); Mt. Pieniny, Sokolka, *J. Walas, Pl. Exs. Pol. 349* (DS, KRA, L, MO, MT, WA); Osim, Swiece, Mizunsa, *D. Woloszezak in 1890* (W); Rybnik, *Ziesche, Fl. Sil. Exs. 603* (WA).

PORTUGAL. Matasinhos, Ponte de Pedra, *J. Castro in 1941* (MA); Serra do Gerez, S Bento da Porta Alberta e Covide, *R. Fernandes & F. Sousa 2625* (DAO, UT); Quinta da Teneria, near Ponte Pedrinha, *A. Fernandes et al. 5365* (TUR, UT); Lloula, Alfochiera, *R. Fernandes & F. Sousa in 1948* (UT); Minho, Braga, Bom Jesus, *C. Fontes et al. 9748* (MT); ca. 1 km N of Avanca, *J. Matos 7591* (TUR); Melaco, S Gregorio, *A. Moller 1377* (WU); near Espinho, between Espinho & Porto, *J. Paiva et al. 7977* (TUR); Arouca, between Arouca and Sohnora da Guia, *J. Paiva et al. 8252* (TUR); Minho, between Valenca & S Gedro da Torre, *M. da Silva 60* (NCU).

ROMANIA. Moldavia, Bacau Dist., near Margineni, *N. Barabas & D. Mititelu in 1970* (TUR, WA); Severin Dist., Buchurest, *P. Cretzoiu in 1936* (MO); Tzahova near Linaia, *Desberger s.n.* (W); Brad, *Dunhoffer in 1891* (WU); Baile Hurculane, *E. Häyren in 1931* (H); Sinaia, *Leitlesberger in 1897* (W); Plolesti Dist., Muntenia, near the town of Sinaia, *E. Lungenson in 1963* (LD); Cotofanesti, Borseni, *D. Mititelu et al. 42* (COLO, DAO, H, TUR, WA); Bals Dist., Oltenia, Oltet valley, *M. Paun 357* (DAO, H, KRA, LD, WU); Transsilvania, Cluj Dist., *I. Prodan 1298* (H, MO, UC, US, W, WA).

SPAIN. Pineta, Campo, *Antiguo s.n.* (MA); Coruna, Santiago de Compostela, *F. Bellot in 1945* (MA); Santander, Espinama, rio Deva, *F. Bellot & B. Casaseca in 1961* (MA); Fuente, Espinama, *F. Bellot & B. Casaseca in 1961* (TUR); Pontevedra, *H. Buch in 1930* (H); Caceras, Banos de Montemayor, *A. Caballero in 1945* (MA); Lugo, Villardiaz-Fonsagrada, *E. Carreira in 1953* (G, MA); Logrono, Canales de la Sierra, *B. Casaseca & F. Diez in 1975* (MA); Pontevedra, Moana, Tiran, *S. Castroviego in 1970* (MA); Navarra, Robledal de Garralda, *I. Caballos & A. Rodriguez in 1960* (MA); Salamanca, Porto de Bajra, *J. Cogolludo in 1914* (MA); Pirineo Orientale, Banos de Ribes, *Costa in 1849* (MA); Villarrube, La Coruna, *F. Diez in 1975* (MA); Louza, Alfocheira, *R. Fernandes & Sousa*

in 1948 (C); Quinta da Teneria, Rio Paivo, *A. Fernandes et al. 5365* (C, LD); Oviedo, Junto a Canisquezo, Sella R., *E. F. Galiano et al. 1661/71* (G); Madrid, Guadarrama, *B. Lazaro s.n.* (MA); Avanca, ca. 1 km N, *J. Matos 7591* (LD); Arredores de Melgaco, S Gregorio, *A. Moller 1377* (LD); Navarra, Burquete, *L. Nee 1784* (MA); between Espinho & Porto, *J. Paiva 7977* (LD); between Arouca & Senhora da Guia, *J. Paiva et al. 8252* (LD); Navarra, Roncesvalles, *C. Pau in 1931* (MA); Pirineos Navarros, Valcarlos, *V. Perez in 1907* (MA); Caceres, Hervas, *S. Rivas-Goday in 1946* (MT); Orense, Castrelo de Mino, *A. Rodriguez in 1935* (MA); Navarra, Alsasua, *H. Roivainen in 1950* (H); Barcelona, Tibidabo Massif, *F. Sennen 3936* (G, LD, MA, W); Santander, Espinama, *C. Vicioso in 1944* (MA); Soria, Agreda, Sierra de Moncayo, *C. Vicioso in 1935* (MA); Estrella, *F. Welwitsch 782* (US).

SWEDEN. Skåne, Röddingekin, *F. Areschoug in 1854* (W); Skåne, Öved, Blommeröd, *E. Asplund in 1928* (MT); Skåne, Örup, *E. Asplund in 1928* (MT); Skåne, Kullaberg, *K. Bergman in 1890* (WTU); Skåne, Kullaberg, Bosjoklöster Parish, *S. Blixt in 1967* (VPI); Öland, Vickleby, *B. Boivin et al. 6988* (DAO); Skåne, Bälteberga, *J. Braun in 1879* (MT); Skåne, Kragehalm, *C. Duréu in 1866* (US); Öland Island, Great Alvar, between Vickleby and Lake Möckelmossen, *F. Fosberg 32693* (US); Skåne, Fastorpskogen, *R. F. Fristedt in 1865* (MO); Skåne, Hasslemölla, *O. Hammar s.n.* (W); Skåne, Ivö, *C. Hammarlund in 1951* (COLO, MO); Skåne, E Sönnarslöv, Maltesholm, *O. J. Hasslow in 1933* (MO); Skåne, Ballinga, *S. Holmdahl in 1946* (TUR); Skåne, Landskrona, *B. Holmgren in 1917* (W); Skåne, Torup, Slottspark, *L. Ikkala in 1946* (H); Öland, Vickleby, *O. Kohler in 1921* (MO, UC); Skåne, Paroecia Södra Sandby, Linnebjärshagen, *N. Johnsson, Pl. Sue. Exs. 1222* (COLO, DAO, H, MTJB, NCU, RSA, W); Skåne, Kullen, *J. Jonsson in 1891* (RM); Uddevalla, *V. Kullgren in 1885* (H); Skåne, Svedala, *A. Magnusson in 1879* (H); Skåne, Börringe, 1 km N of Havgård, *K. N. Mattisson 1467* (DAO); Skåne, Torup, *E. Rathsman in 1968* (MO, SMU, UC); Göteborg, *E. Rehnberg in 1888* (W); Västergöteland, Vänersnäs, Munkesten, *J. A. Ryde in 1884* (MO); Bohuslän, Lyse Parish, Alsbäck, *G. Samuelson in 1900* (NO, MT); Skåne, Horby, *S. Selander in 1905* (WS); Skåne, Kullen, *S. Selander in 1907* (TEX); Västergöteland, Halleberga, *G. Svensson in 1937* (UC); Skåne, Helsingborg, *G. Turesson in 1908* (H, TUR); Kulla Gunnarstorp, *R. Wallengren in 1874* (H); Skåne, Brunby, *W. Wallengren in 1885* (H); Skåne, Kullen, *F. G. Widgrene in 1864* (UC).

SWITZERLAND. Basell, forest by Schauenburg, *P. Aellen in 1932* (MO, NDA, UT); Eschenberg, *G. Bachmann in 1892* (Z); Fribourg, *F. Castella in 1904* (US); Zurich, Marthalen, *L. Farrer in 1908* (Z); Höngger Berg, *H. Grassmann in 1913* (UC); Ringgenberg, vicinity of Interlaken, *Hegi in 1829* (US); Fribourg, Cernias, *Jaques in 1903* (COLO); Schaffhausen, Guntmadingen, *E. Kelhofer 1559* (Z); Aquila, *R. & A. Keller in 1902* (Z); Zurich, *W. Koch 39/625* (TUR); Clairiere, at the foot of Henberg, *G. Kohler in 1919* (WTU); Appenzell-Innerrhoden, Büchaugabrüff, *A. Koller in 1918* (Z); Vitznau on Lake Lucerne, *G. Miller in 1904* (CAS, RM, US); Kusnacht, *F. Oppliger 375* (Z); Vaud, Lausanne, *P. Pfister in 1949* (US); Bex, *Schleicher s.n.* (MO, UC); Winterthur, Eschenberg, *H. Siegfried in 1882* (Z); Chrischone, near Basel, *T. L. Steiger in 1932* (NEB); Fribourg, Gruyeres, Cernias, *T. Taquet in 1903* (Z); Geneva, Commune de Vandoeuvres, *S. Vautier et al. 557* (DS, GA, MA, NCU, PH, RSA, SMU, TUR, UBC, UC, US, WS, WTU); Gsental in Pilatus, *M. Vischer in 1910* (Z); Martigny, *F. P. Wolf in 1886* (Z).

UNITED KINGDOM: ENGLAND. Knowsley, between Liverpool & Prescott, *M. Atkinson in 1959* (W); Whitton, *A. E. Baggs in 1910* (UBC); Windermere, Westmorland, *J. Ball in 1876* (PH); Gloucestershire, St. Briavels, *J. Ball in 1854* (US); Westmorland, Rydal, *J. Ball in 1838* (IA); Cheshire, *A. Bennett in 1883* (MTMG); Lynton, *E. Brubaker 1949* (PENN); Surrey, 1 mi. NE of Dorking, *R. Brummitt 60362* (W); Ambleside, *R. Campbell s.n.* (MTMG); Parkstone, Dorset, *M. Cocke 12* (MTMG); Chislehurst, *J. Cockerell s.n.* (NMC); Marlow, Davenport Wood near V. C. 24, *M. B. Gerrans 1357* (ASU, H); Isle of Wight, *Harland s.n.* (IA); Clovelly, *E. & S. Harper in 1901* (US); Surrey, Morden Hall, *C. Hartman in 1849* (W); Cheltenham, *T. J. Hatton in 1830* (UMO); Cornwall, St. Anthony in Roseland, near Truro, *G. Hayes 47* (W); Essex, Berechurch, *S. T. Jermyn 229* (DAO); London, Regents Park, *Y. Mäkinen in 1960* (TUR); Kent, Bromley, *C. Marchant in 1955* (UBC); Surrey, Box Hill, *A. Melderis & E. B. Bangerter 126* (DAO); Yorkshire, *R. Middleton in 1858* (MTMG); Durham, *R. Middleton in 1845* (MTMG); Cambridge, *J. H. Newton in 1965* (NCU); Surrey, Cooper's Hill, Runnymede, *D. Philcox 2152* (ASU, SMU); Addingsham, *F. Rhodes in 1906* (PENN); Cornwall, Penzance, *N. Taren in 1961* (TUR); Wickham, Hants, *T. M. C. Taylor 5560* (UBC); Cornwall, Lostwithiel, *E. Thurston in 1929* (MO, US); York, Wetherby, *G. Webster in 1879* (MIN); Bristol, Clifton, *J. White in 1929* (CAS, SMU); Middlesex, Tottenham, *B. Wurzell 973* (MO). IRELAND. Limerick County, *W. Cleburne in 1882* (NEB); Kerry County, Killarney, Muckross Estate, *P. Halliday 55* (DAO); 5 mi. W of Sligo, S side of Knocknarea, The Glen, *A. C. Jermy 1476* (RSA); Killarney, Ross Island, *H. Lindberg in 1932* (H); Galway County, Lough Derg, *A. E. Lomax in 1886* (DS); Dublin County, Lucan?, *M. O'Leary in 1939* (SMU, TUR); Wicklow County, Devil's Glen, *M. Scannell in 1950* (H); Meath County, River Boyne, Donore, Drogheda, *D. Synnott in 1963* (TUR). SCOTLAND. Tyfe, *J.*

Cruickshank in 1837 (US); Aberdour, *Gunn 138* (UBC); near Abbotsford, *I. M. Hayward in 1912* (OKLA); Midlothian, The Yore, Yorebridge, *J. Sinclair 2346* (NCU); Arran Island, *Wrightshar in 1861* (UC); Lanark, *without collector in 1872* (E). WALES. Arthog, Merionethshire, *P. Benoit in 1953* (MT); Tregwynt, *R. Campbell in 1890* (MTMG); Glamorganshire, *R. L. Smith in 1928* (OKL); Porthkerry, Glamorgan, *A. E. Wade in 1937* (B).

YUGOSLAVIA. Serbia, Knjazewac, *Adamovio in 1896* (WU); Serbia, Kopaonik, *M. Dimitrijin in 1883* (WU); Serbia, Rtanj, *M. Dimitrijin s.n.* (WU); Slavonia, Papok Mts. near Pozega, *A. Ginzberger in 1910* (WU); Serbia, Nakrivanj, *G. Ilic 1184* (WU); Serbia, Nisch, *G. Ilic 1090a* (WU); Croatia, Crnopac, *E. Janchen in 1907* (WU); Bosnia, Plitvice, *H. Lenander in 1938* (RM); Herzegovina, Nevesinje, *H. Raap 176* (H, LD, US, WU); Bosnia, Hsan, *J. Schiller in 1903* (WU); Croatia, Plitvice, *J. Schiller & M. Stark in 1902* (WU); Serbia, Beograd, *T. Wisniewski & H. Sliwinska in 1927* (WA).

AFRICA

ALGERIA. Without locality, *J. A. Batandier s.n.* (G); Oran, *E. Bjorling in 1882* (L); Blivah, Chiffa Gorge, *E. Cosson in 1854* (GH, MO, W); Foot of Oved, Guelil, near Grotte Marveilleuse, *Davis 52838* (RNG).

TUNISIA. Ain Draham, *Thebault in 1910* (G).

U.S.S.R.

ARMENIAN S.S.R. Surnuchi, Uzen-Mesa, *A. Schelkovnikov & E. Kara-Murza in 1929* (LE); Kasrapekeiy Region, *Zpuzopan in 1959* (W). AZERBAIJAN S.S.R. Kuba, near Kusary, *S. Grigoriev 8* (DS); Hzejbedzanskaya, Zanabatskyi, 9 km from Zaradat, *I. Ilinskaja in 1946* (LE); Langelan, between Ordaklyu and Sabu, *Y. Karjagin & A. Chadarin in 1932* (S); Lenkovanskyi Dist., Alekseevka, *M. I. Kurmoshkin in 1936* (LE). BELORUSSIAN S.S.R. Minsk Prov., Czervenski, Igomenski, *Savicz et al. in 1930* (MW). GEORGIAN S.S.R. Mekvena, at the Riova R., *A. & V. Brotherus in 1877* (H); Caucasus, between Tkue & Kosekha at Didi Liachva, *A. & V. Brotherus 342* (BM, H (mixed sheet with *C. alpina* and *C. × intermedia*)); Caucasus, S Osetiya ("Osebia"), near Falkudschin, *E. & N. Busch in 1928* (S); Abkhasia, Sukhumi, *P. H. Davis 33672* (K); Adzhariya, *A. Dimitrieva in 1965* (NA); Abkhazskaya, Gareiniskiy Khrebet, *C. R. Frazer Jenkins 2906* (BM); Kutaiskaya, Guri, *E. I. Kikodse in 1914* (GH); Caucasus, Batum Dist., Zelenom Misu, *P. N. Krilov & E. I. Steinberg in 1916* (LE); Tzebeld Dist., Azbijanskyi, *J. Menitzkyi 197* (LE); Transcaucasus, Cartalinia, Borshom, *Olearski in 1909* (DS); Caucasus, Abkhazia, Tsebeldie, Terjevskoya, *Voronova in 1905* (S, US). LITHUANIAN S.S.R. Kaunas, B. Hryniewiecki in 1929 (WA). MOLDAVIAN S.S.R. Strashensky region, *A. Borisova 1520* (DAO); Strashensky, Kupriani, *A. Borisova 1520a* (MW); Korneshty, upper Redjanski valley, *A. Borisova 1681* (MW); Ungenski Dist., St. Redeni, *E. Lipovaya in 1959* (A, H). RUSSIAN S.F.S.R. Yaroslav, Rybinski, Kameniki village, Niznenikulski, *B. A. Fedchenko et al. in 1923* (MW); Moscow Dist., Kuntzevo, *M. Koshevnikova 817* (H, MW, W, WA); Kostroma Prov., Nerehtsk, Vasilevo, *K. K. Kossinsky 819* (MW); Soczi Dist. Krassnaya-Polyana, *D. Litvinov 213* (G, H, LE, W, WA, WU); Kaliningrad Prov., Kresno Armenskaya, *A. Poledimova & Czerepatov 535* (MW); Kuban R., *Poltaintsay in 1889* (WU); N Caucasus, Maykop, *N. Shestounow 1220* (NY); Penza Prov., Mokshansk, *Sprygin in 1909* (MW); Mts. near Moscow, *Tchikorsky s.n.* (W). UKRAINIAN S.S.R. Krym, Czatyrdag Mt., *E. O. Belanskaya et al. in 1968* (MW); Mukachevo, *V. Grubov & E. Rachkovskaya in 1949* (DS); Transkarpat, opposite city of Perechin, *K. N. Igoshina & A. A. Benken in 1951* (MW); Volinsk, Kremenets, *A. I. Micholson in 1916* (MW); Transcarpatia, Rachov Dist., *G. Ogureena in 1959* (MO); Bila Tzerkova Dist., Luka, *E. Palonska in 1929* (S); L'vov (Lyvov) Prov., Czertova Mts., Virniki, *A. I. Pojarkova et al. in 1940* (MW); Krym, Romanovskaya Highway, *H. Poplawska 883* (MW); Krym, Mt. Tschatyrdagh, *V. Siplivinski et al. in 1968* (MO); Krym, Buka, between Mts. Demordnis & Tschartyrdagh, *A. K. Skvortsov in 1967* (MO); Transcarpatia, Veliki] Berezny, *A. K. Skvortsov in 1968* (MO); Krym, Mons Babugan, *A. K. Skvortsov in 1969* (MO); Transcarpatia, Mukascherv, *A. K. Skvortsov in 1969* (MO).

ASIA

IRAN. Mazanderan, S of Amol, *J. C. Archibald 2287* (K); Ghilan, *Aucher-Eloy 4909* (BM, G, P, W); W Elburz, N side of Kandevan Pass, *Bowles Bot. Exped. 2258* (K); Khurasan, 80 mi. ENE of Gorgan near Bojnurd Road, *Furse & Synge 523* (K); Mazanderan, 8 km S of Chalus, *M. Grant 16494* (NA); Mazanderan, Gozlu, *W. Koelz 16237* (US); Guilan, Lahijan, *N. Lindsay 863* (BM, MO); Rosht, *H. Pravitz 957* (S); Mazanderan, Chalus R. valley, *K. Rechinger 2066* (US); Ostan 2, Khozlok & Gurgan, *F. Schmid 6021* (G); between Gagan & Bojnurd, *without collector 3997* (K); Mazanderan, Haraz valley, Karehsang, *P. Wendelbo 1515* (DS).

SYRIA. Mt. Amanus, *M. Haradjian 158, 4582* (G), *234* (G, K); Amanus, Mt. Dumauly, *M. Haradjian 3733* (G).

TURKEY. Kilidjbounar, Bagtchekeuy, *G. V. Aznavour in 1900* (G); between Beycos & Akbaba, *G. V. Aznavour in 1890* (G); Findiksou, *G. V. Aznavour in 1899* (G); Sariyer, Kastanesouyose, *G. V. Aznavour in 1895* (G); Findik & Kestane Souyou, *G. V. Aznavour in 1895* (G); Lazistan, Rhize, *B. Balansa in 1866* (G, K); Rize, Hemsin, Meydan Kobaca, Mollaveysa, *P. H. Davis 21381* (BM); Uniye, Uniye-Karakus, *P. H. Davis & O. Polunin 24919* (BM, K); Coruh (Artvin), Savval Tepe, Murgul, *P. H. Davis & I. C. Hodge 32216* (BM, K); Zonguldak, Tefenni to Yenice, *P. H. Davis et al. D37755* (K); Trabzon, Bos Tepe, *F. Handel-Mazzetti 200* (W); Alma Dag, *M. Haradjian 158* (W); Istanbul, Belgrad Ormani, *B. Kasaplyrl 564* (UC); Amasya, Akeziwan, *Manisadjan 201* (K, S); Bolu, Adapazari (Sakarya)-Bolu, *McNeill 240* (K); Polonezkay, *B. V. D. Post in 1939* (G); Rize, Black Sea, *B. V. D. Post 2020* (G); Thrace, Ketcheli, *H. G. T. in 1930* (K); Black Sea coast, ca. 20 mi. W of Trabzon, *P. Votila 19863* (H).

Plants intermediate between *Circaea lutetiana* L. subsp. *lutetiana* and *C. lutetiana* subsp. *quadrisulcata* (Maxim.) Asch. & Mag.:

AUSTRIA. Osttirol, SE of Dolsach, *A. Polatschek in 1976* (W).

U.S.S.R. BELORUSSIAN S.S.R. Vitebsk Prov., vicinity of Vasuty, *N. Koslovskaja 597* (MW). LATVIAN S.S.R. Duna R., near Kokenhusen, *Bruttan 272* (MW). RUSSIAN S.F.S.R. Ufa Prov., vicinity of Durrassowo, *I. Schirajewsky in 1907* (MW). UKRAINIAN S.S.R. Mogilev Prov., between Mogilev & Borysthenem, *N. Downar in 1862* (MW); Chernigov Prov., vicinity of Starodub, *Rogovich s.n.* (MW).

Circaea lutetiana subsp. *lutetiana* can be distinguished by the presence of an exserted, nectar-secreting disc, the bilocular, clavate to obovate fruits that lack prominent ribs and sulci, by the pubescent stems, and by a generally longer, more slender floral tube than in other species of the genus.

Circaea lutetiana subsp. *lutetiana* differs from subspp. *canadensis* and *quadrisulcata* in dimensions and morphology of the fruits and in length of the floral tube, although there is some overlap in the latter character. *Circaea lutetiana* subsp. *canadensis*, in addition to its isolated range from the other two subspecies, almost always has a minute bracteole at the base of the pedicels. Both *C. lutetiana* subsp. *canadensis* and subsp. *quadrisulcata* tend to have glabrous stems but occasional plants of subsp. *quadrisulcata* have a few, widely scattered falcately recurved hairs on the upper internodes. *Circaea lutetiana* subsp. *lutetiana* commonly has ovate leaves while the leaves of subspp. *canadensis* and *quadrisulcata* are more consistently oblong ovate.

Numerous infraspecific taxa have been proposed (see synonymy) to account for the variability that occurs within *Circaea lutetiana* subsp. *lutetiana* but these names have been based primarily on studies undertaken in limited geographical areas and have not taken into account plants from throughout the entire range of the subspecies. When this is done, it is clear that the numerous subspecies, varieties, and forms do not exhibit any geographical or ecological pattern and do not warrant formal taxonomic recognition. Relatively few specimens have been examined during this study, but a selection is cited here.

The presence of bracteoles, which Ascherson and Magnus (1870) used to describe *Circaea lutetiana* subsp. *mediterranea*, as with other characters, is highly variable. Plants with bracteoles do not occur exclusively within a well-defined geographical area although plants with bracteoles tend to be more common in the region around the Mediterranean. Raven (1963) found no plants of *C. lutetiana* with bracteoles from the British Isles. In *C. lutetiana* subsp. *lutetiana*, bracteoles,

TABLE 1. Comparison of *Circaea lutetiana* subspp. *canadensis*, *quadrisulcata*, and *lutetiana*.

		C. lutetiana subsp. *lutetiana*	*C. lutetiana* subsp. *canadensis*	*C. lutetiana* subsp. *quadrisulcata*
Pedicel	flower	2–9 mm	2–6 mm	1.9–4(–5*) mm
	fruit	3.8–10 mm	3.5–6.5 mm	3.5(–6.3*) mm
Bud	length	2.4–5.4 mm	2.3–4.1 mm	2.6–3.8 mm
	width	1–1.9 mm	1.2–2.3 mm	1.1–1.5 mm
Ovary	length	1.1–2.2 mm	1.2–1.7 mm	1–1.7 mm
	width	0.9–1.5 mm	0.8–1.3 mm	0.8–1.1 mm
Floral tube	length	0.8–2.4 mm	0.4–1.2 mm	0.6–1 mm
	width	0.1–0.3 mm	0.2–0.3 mm	0.2 mm
Sepals	length	1.6–4.5 mm	1.9–3.8 mm	1.3–3.2(–3.5*) mm
	width	0.8–2 mm	1.2–2.4 mm	1–1.7 mm
Petals	length	1.4–3.5 mm	1.3–2.9 mm	1–2(–2.5*) mm
	width	1.8–4 mm	1.5–4 mm	1.4–2.5 mm
Apical notch		0.6–2.4 mm	0.4–1.7 mm	0.4–1.2 mm
Filaments		2.5–4.3 mm	1.2–2.8 mm	1.6–3.5 mm
Anthers	length	0.6–1 mm	0.6–0.8 mm	0.3–0.7 mm
	width	0.3–0.9 mm	0.5–0.8	0.3–0.5 mm
Style		3.3–6 mm	2.2–5.5 mm	1.8–4.2 mm
Stigma	length	0.2–0.6 mm	0.2–0.4 mm	0.2–0.4 mm
	width	0.4–0.9 mm	0.3–0.6 mm	0.3–0.6 mm
Fruit	length	2.8–3.8 mm	2.8–4.5 mm	2.2–3.8 mm
	width	1.4–2.4 mm	1.9–3.6 mm	1.8–3(–3.4*) mm
Pedicel + fruit		6.3–15 mm	6.3–11.2 mm	4.3–8.5(–10*) mm
Leaf	length	3–15 cm	5–16 cm	4.5–12 cm
	width	2–12 cm	2.5–8.5 cm	2–5 cm
Petiole		0.6–7.5 cm	1.3–5.5 cm	1.5–5 cm
Disc	length	0.2–0.6 mm	0.3–0.7 mm	0.2–0.6 mm
	width	0.3–0.9 mm	0.6–1.1 mm	0.5–1 mm
Fruit shape		clavate to obovoid	pyriform to subglobose	pyriform to subglobose
Stem pubescence		usually dense	glabrous	glabrous to very sparse

* Measurements from plants collected north of the Altai Mountains in central Siberia.

when present, are often restricted to the lowermost pedicels or, if present at the base of all pedicels, are deciduous before maturation of the fruit. Only rarely are bracteoles somewhat persistent below all pedicels of an inflorescence. Table 1 compares the subspecies of *C. lutetiana*.

5. Circaea erubescens Franchet & Savat., Enum. Pl. Jap. 2: 370. 1879.—FIG. 15.

Circaea delavayi H. Lév., in Fedde, Rep. Nov. Sp. 8: 138. 1908. TYPE: China, Sichuan, Chien-feng-shan, forests of high mountains, August 1894, *J. M. Delavay 5021* (G, lectotype; DS, G, P,

isolectotypes). The label data on Delavay's collection is "Yunnan, Tchen-fong-chan." The only name in the area of this collection that approximates the pronunciation of Delavay's "Tchen-fong-chan" is Chien-feng-shan in southern Sichuan, just south of the Yangtze River, but near northeastern Yunnan.

Circaea lutetiana L. race *erubescens* (Franchet & Savat.) H. Lév., Bull. Acad. Int. Géogr. Bot. 21: 219. 1912.

Circaea kawakamii Hayata, Icon. Pl. Formos. 5: 71. 1915. TYPE: China, Taiwan, T'ai-tung Hsien, Mt. Hito-shan ("Ritozan"), August 1913, *T. Kawakami* (TAIF 18267, lectotype; TI, isolectotype; A, US, photograph).

Erect, or decumbent at the base and rooting at the nodes, 1–12 dm tall, simple or freely branched above, forming numerous, sometimes branched, rhizomes without tuberous thickenings that give rise to the following year's plants from their tips. Plants glabrous or, in some plants from Japan and from Cheju-do (Quelpaert Island), Korea, the stem finely pubescent with soft, short, falcately recurved hairs, 0.1–0.2 mm long, these continuing along the petioles, where the hairs are upwardly curved, to the under, and sometimes also the upper, surface of the leaves. Nodes, rarely the entire stem, deep reddish-purple. Leaves horizontally spreading, commonly reddened between the veins, opaque: those between the middle and upper part of the stem the largest, (2.5–)4–8(–10) cm long, (1–)2.3–4.5(–6) cm wide, becoming gradually to abruptly reduced in size upward and eventually bractlike and opposite or subopposite, rarely alternate, in the lower part of the inflorescence, gradually reduced in size downward; lanceolate to ovate or occasionally broadly ovate, short acuminate at the apex, very broadly cuneate to rounded or truncate, rarely subcordate, at the base, denticulate. Petioles (0.6–)1.5–4(–6) cm long, terete or semiterete, often with reduced branches arising in the axils. Inflorescence glabrous, a simple terminal raceme or, more commonly, with additional racemes at the tips of the uppermost axillary branches; the racemes simple or, more commonly, branched at the base, the branches alternately or oppositely arranged, subtended by reduced leaves or leaf-like bracts. The terminal raceme, from the uppermost reduced leaf or leaf-like bract, ca. 2 cm long at initiation of flowering, to 20 cm long at cessation of flowering, the lateral racemes ca. 2 cm long at initiation of flowering, to 17 cm long at cessation of flowering, the lateral branches often of unequal lengths on the same plant. Flowering pedicels (1.5–)2.5–5.5(–7) mm long perpendicular to the axis of the raceme, without, less commonly with, a minute, setaceous bracteole, 0.1–0.4 mm long, at the base which is usually deciduous before maturation of the fruit. Fruiting pedicels 4–8.5 mm long. Buds glabrous, reddish-purple, narrowly elliptic to oblong or oblanceolate in outline, gradually tapering to abruptly short or long acuminate at the apex; from the summit of the ovary, 2.4–3.2(–3.6) mm long, 0.8–1.5 mm thick just prior to anthesis. Ovary 0.7–1.2 mm long, 0.5–0.9 mm thick at anthesis, narrowly to broadly obovate in outline, densely pubescent with translucent, soft, uncinate hairs. Floral tube 0.5–0.8 mm long, ca. 0.2 mm thick at the narrowest point, cylindrical or narrowest at the middle and dilated at both ends. Sepals 0.6–2.5 mm long, 0.8–1.2 mm wide, glabrous, reddish-purple, oblong to lanceolate, abruptly short to long acuminate, reflexed in flower. Petals 0.8–1.7 mm long, 0.7–1 mm wide, longer than wide, pink, narrowly to broadly obtrullate or obovate in outline; the apical notch 0.1–0.3 mm deep, $^1/_{10}$–$^1/_5$ the length of the petal; the petal lobes very minutely crenulate or with minute secondary lobes, closely spaced; the petals tapering smoothly to the base. Stamens spreading at anthesis or rarely one, very rarely both, appressed to the style; shorter than the

style; filaments 1.4–2.3 mm long; anthers 0.4–0.7 mm long, 0.2–0.5 mm thick. Style straight, erect or slightly drooping at the apex, 2.2–3 mm long, topped by an obtriangular to transversely oblong stigma, 0.1–0.4 mm tall, 0.3–0.5 mm thick. Nectary exserted as a conspicuous, fleshy, cylindrical disc, 0.2–0.5 mm tall, 0.3–0.6 mm thick. Mature fruit 1.7–3.2 mm long, 1.2–2.1 mm thick, bilocular and 2-seeded, obovoid to broadly so, very slightly flattened dorsally, broadly rounded at the apex, tapering smoothly to the pedicel, without prominent ribs or sulci but with a narrow groove representing an extension of the pedicel; densely covered with stiff, translucent, uncinate hairs, ca. 0.6 mm long, and with fewer, shorter, capitate and clavate-tipped glandular hairs ca. 0.1 mm long. Fruiting pedicels slightly to sharply reflexed. Combined length of pedicel and mature fruit, (6–)7.5–12 mm long. Gametic chromosome number, $n = 11$.

TYPE: Japan, Kanagawa Prefecture, Mt. Hakone, August 1866–1874, *P. Savatier 413* (P, holotype).

Distribution (Fig. 14): Rocky streambeds and seepages, along trails and road banks and rich alluvial woods in temperate deciduous forests. Japan, except Ryukyu Islands and islands south of the Kyushu mainland; South Korea; China, from Jiangsu and Zhejiang westward along the Yangtze River and its tributaries to southern Sichuan, Yunnan, and Guizhou; Taiwan. From near sea level to 2,500 m. Flowers, from mid-June through August and sporadically to mid-September.

Representative specimens examined:

U.S.S.R.

RUSSIAN S.F.S.R. The single specimen from the Soviet Union, Siberia, above Kulsuk (Kyrmykr), at the middle part of L. Baikal, *S. J. Enander in 1913* (S), is obviously the result of mixed collections. Enander visited Japan during the same year and presumably collected this specimen there. Other reports of *Circaea erubescens* from Sakhalin have been clarified by Skvortsov (1979), who pointed out that those collections are *C.* × *intermedia*.

ASIA

CHINA. ANHUI: Huang Shan, *R. C. Ching 4178* (UC), *8567* (US); W Siunin, Ma-che, *R. C. Ching 4460* (UC), *8840* (US); Huang Shan, *K. S. Chow 486* (PE); Jinzhai Hsien, *Colleagues Bot. Inst. E China Sta. 6780* (PE); Hiu Keou, *P. Courtous 37725* (NAS); Huang Shan, *L. K. Fu 748* (NAS, PE); Jinzhai, *Stat. Bot. Est. China 6780* (NAS). FUJIAN: Wuyi Shan, *C. P. Tsien 401002* (PE). GUANGDONG; Ruyuan Hsien, *X. G. Li 201148* (PE). GUIZHOU: Lung-li Mts., *J. Cavalerie 3840* (E, K, P); Fang-ching Shan, *C. Y. Chiao & C. Cheo 454* (NAS); Yinchiang Hsien, *T. P. Chien 31709* (PE); Jungchiang Hsien, *T. P. Chien 51787* (PE); Rongjian, *Exped. S Guizhou 3269* (NAS); Fanjing Shan, *Guizhou Exped. 1675, 2222* (PE); Ta-ho-yen, Mt. Fanjing Shan, *A. N. Steward et al. 454* (E, GH, L, NY, PE, S, US); Ma-tsoong-ling, Tuyun, *Y. Tsiang 5785* (NAS, NY, W); Tuyun, *Y. Tsiang 5998* (NAS, NY, W); Sihfeng, *Y. Tsiang 8126* (NAS). HUBEI: Lichuan Dist., Suisapa (*Metasequoia* area), *W. C. Cheng & C. T. Hwa 842* (K, UC); Jianshi Hsien, *L. Y. Dai 1301* (PE); Badong Dist., Yichang, *A. Henry 4743* (LE); S Badong, *A. Henry 7279* (K, LE); Hegeng Hsien, *H. J. Li 5787* (PE). HUNAN: Nanyuen, *Y. Liu 168* (NAS); "Hunan," *S. Z. Sin 236* (PE). JIANGXI: Shangyou Hsien, *T. L. Chia 521, 70533* (PE); Lu Shan, *Y. K. Hsiauog? 6727* (NAS), *H. H. Hu 2473* (PE); Lu Shan–Kuling, *A. N. Steward 963* (UC); Lu Shan, *M. J. Wang 842* (NAS). JIANGSU: Nanjing, *Macklin 33a* (GH). SHAANXI: Foping Hsien, *K. T. Fu 5076* (PE). SICHUAN: Wan Hsien, *W. C. Cheng & C. T. Hwa 842* (PE); Chengkuo Hsien, *T. L. Dai 101845* (PE), *104641* (NAS, PE); "Tchen-fong-chan," *J. M. Delavay in 1893* (MO, P, US), *5176* (DS, G, P); Mt. Emei Shan, *E. Faber 71* (K, US), *303* (MO, P), *W. P. Fang 3138* (E, K, P, PE, US); Ebian Hsien, *Y. Y. Ho 6487* (NAS); Shimian Hsien, *C. C. Hsieh 42284* (PE); Nan-ch'uan Hsien, Chin-shan t'eh-wa-shih, *C. H. Hsiung & T. L. Chou 92747* (PE); Nanchuan Hsien, *K. F. Li 62928* (NAS, PE); Opien Hsien, *C. L. Sun 946* (US); Mt. Emei Shan, *S. C. Sun & K. Chang 878* (A); Hanyuan Hsien, *T. P. Wang 8652, 8820* (PE); Nanchuan Hsien, *J. H. Xiong 91837, 92109, 92374, 92747* (PE); Emei Hsien, *K. H. Yang 56347* (NAS, PE); Ebian Hsien, *Z. W. Yao 2872, 3002*

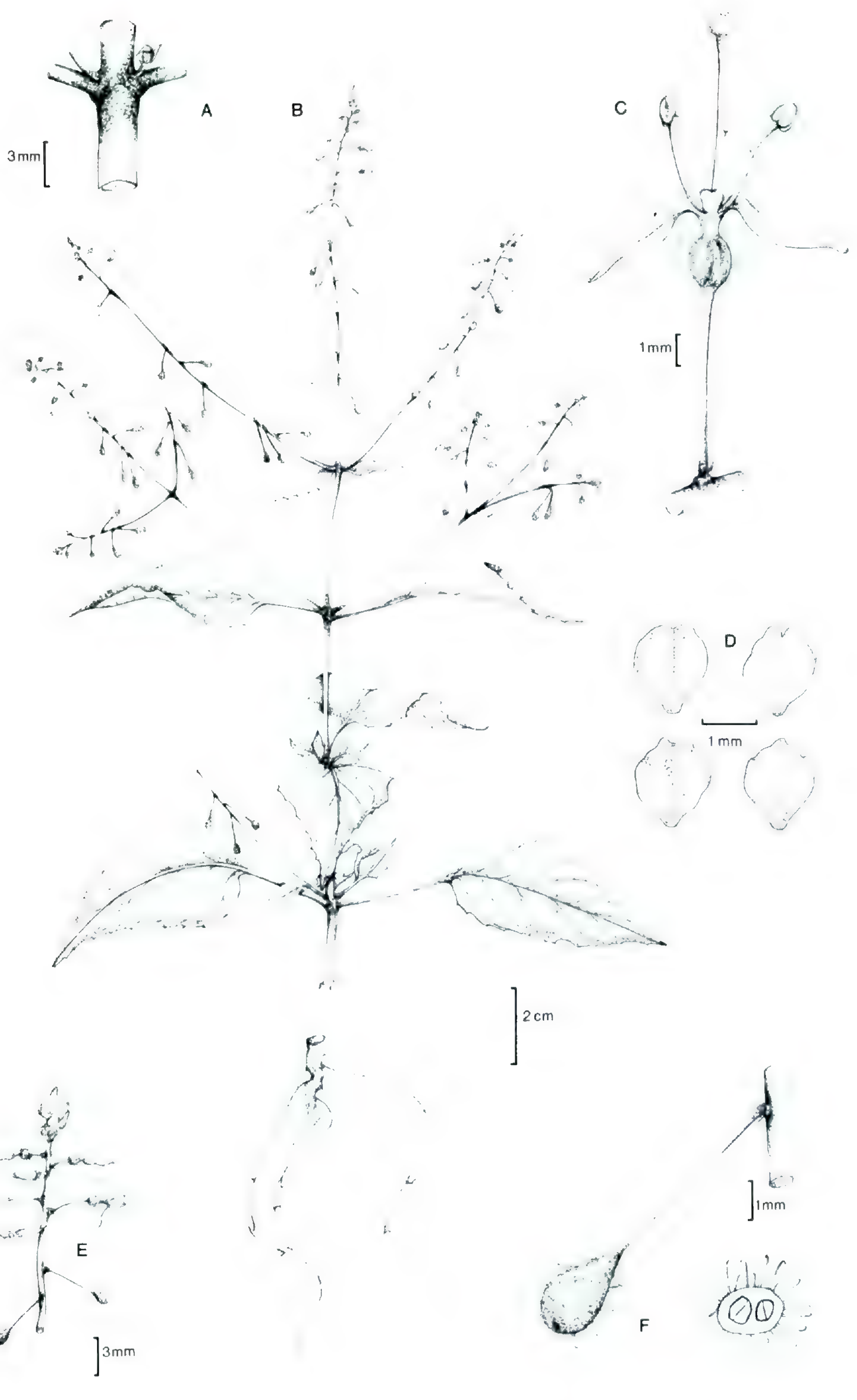


FIGURE 15. *Circaea erubescens* Franchet & Savat.—A. Mid-stem node.—B. Habit.—C. Flower with petal removed; note exserted nectary.—D. Variation in petals.—E. Inflorescence.—F. Fruit. From *Boufford & Wood 19860* (KYO, MHA, MO).

(PE), *4531* (NAS, PE). TAIWAN: Kwarenko-cho, Tyuosen-zan, Rodohu-tobe, *Fukuyama & T. Suzuki in 1936* (TAI); Hsinchu Hsien, Kwan-wu, Chuton Logging Station, *T. C. Huang 4142A* (TAI); Hualien Hsien, Luan Shan, *T. C. Huang 4142A* (TAI); Ilan Hsien, Mt. Nan-ko-tai-zan, *Kojima & Shiomi 2025* (KYO); Mt. Rara, *E. Matuda in 1918* (TI, UC); Taipei Hsien, Uusan (Wu-shan?), *E. Matuda in 1918* (TAIF); Ilan Hsien, Mt. Nan-ko-tai-zan, *J. Ohwi in 1933* (KYO), *3910* (K, TNS); Taitung Hsien, Mt. Rito, *S. Sasaki in 1913* (TAI); Hsinchu Hsien, Taiping Shan, *S. Sasaki in 1915* (TAIF); Ilan Hsien, "Nan-hu-ta-shan," *S. Sasaki in 1922* (TAI, TAIF); Hsinchu Hsien, Mt. Yura, *Y. Simada 2059* (TI), *2423C* (TAI), *2423D* (NTUF); Ilan Hsien, Mt. Nankotaizan, *S. Suzuki in 1922* (KAG); Taiheizan, *S. Suzuki in 1928* (NAS), *in 1929* (GH); between Matomine & Hakko, *S. Suzuki in 1930* (PE); Mt. Taiheizan, *S. Suzuki 1107* (PE); Sanyaku & Suigen, *S. Suzuki 5941* (TAI); Nantou Hsien, from Ali Shan to Hoshe, *M. Tamura et al. 22237* (S, SHIN); Hualien Hsien, Mei-ma-wang-shan, *S. Ying 1306* (NTUF); Hsinchu Hsien, Mt. Tai-ping-shan, *without collector in 1929* (TAI); Xinzhu Zhou, *without collector in 1932* (NAS). YUNNAN: Daguan Hsien, *NE Yunnan Exped. 192* (PE); Yiliang, *NE Yunnan Exped. 851* (KUN). ZHEJIANG: Mt. Tientai Shan, *C. Y. Chiao 14465* (E, UC, US); Hsi-tienmu Shan, *H. C. Chu 238* (NAS), *Exped. Pl. Res. Zhejiang 29470* (NAS); Tiantai, *Exped. Pl. Res. Zhejiang 28118* (NAS); Hsi-tienmu Shan, *Y. Y. Ho 678, 22450, 25307, 54587* (NAS); Changhua, *Y. Y. Ho 23921* (NAS); Tianmu Shan, *K. C. Kuan 75450* (PE), *T. N. Liou 6959* (NY, PE); Mt. Hsi-tienmu Shan, *H. Migo in 1935* (TI); Tianmu Shan, *H. Migo in 1935* (PE), *K. K. Tsoong 621* (PE); "Chekiang," *without collector 20168* (WH).

JAPAN. HOKKAIDO: around Hakodate, *Albrecht in 1861* (LE); Sapporo, *S. Arimoto in 1902* (MO); Hidaka, Shizunai-cho, ca. 14 km ENE of Shizunai, *D. E. Boufford & E. W. Wood 19676* (BM, CM, G, K, KYO, LD, MHA, MO, NCU, PE); Hidaka, Samani-gun, Samani-cho, Okada, *D. E. Boufford & E. W. Wood 19690* (BM, CM, G, GH, K, KYO, MHA, MO, NCU, PE, TUS); Kushiro, Kawakami-gun, Shibecha Experimental Forest of Kyoto Univ., *D. E. Boufford & E. W. Wood 19764* (CM, E, K, KYO, MHA, MO, PE, UC); Abashiri, Yubetsu-cho, 1.6 km E of Engaru-cho on hwy 147, *D. E. Boufford & E. W. Wood 19796* (CM, K, KYO, MHA, MO, PE); Kawakami, hwy 40 just WNW of Osashima, *D. E. Boufford & E. W. Wood 19835* (MO); Sorachi, Ashibetsu city, along the Hachigatsu-gawa R., *D. E. Boufford & E. W. Wood 19854* (BM, C, CM, G, GH, K, KYO, LD, MHA, MO, NCU, P, PE, TUS); Ishikari, Sapporo city, *D. E. Boufford & E. W. Wood 19860* (KYO, MHA, MO); Poronai, *W. P. Brooks in 1884* (UC); Hakodate, *U. Faurie 1339* (KYO); Horobetsu, *U. Faurie 2631* (KYO, P); mountains of Sapporo, *U. Faurie 3165* (P); Hidaka, Saruru, *T. Fujita & E. Nakagawa in 1955* (TUS); Ishikari, Sorachi-gun, Manju, *F. C. Greatrex in 1915* (SAP); Oshima, Narukagawa valley, *F. C. Greatrex 339* (SAP); Shiribeshi, Mt. Karibu, *F. C. Greatrex 339a* (SAP); Hidaka, Shoya, *H. Hara in 1934* (ORE); Hidaka, Horoizumi, Shoya, Maruyama, *H. Hara et al. in 1974* (TI); Toyobishi, *S. Hori s.n.* (SAP); Ishikari, Mt. Yubari, *R. Ishida in 1928* (UC); Kushiro, Mt. Meakan, *T. Kawakami in 1897* (SAP); Teshio, Kami-otoineppu, *G. Koidzumi in 1930* (KYO); Hidaka, Shizunai-gun, from Petakari-sanso to the base col of Mt. Petakari, *H. Koyama & N. Fukuoka 3257* (KYO): Mororan, *T. Makino in 1899* (COLO); Toya-mura, Iburi-koku, *T. Makino s.n.* (KAG, MAK 6945, S); Shiribeshi, Okushiri Island, *S. Matsuda 876* (KYO); Moiwa, *S. Matsumura in 1899* (TI); Ishikari, Sapporo, *K. Miyabe in 1882* (PH); Oshima, Ichinowatari-sanchu, *K. Miyabe & Y. Tokubuchi in 1890* (SAP); Oshima, Shiriuchi-sando, *K. Miyabe & Y. Tokubuchi in 1890* (SAP); Shiribeshi, Okushiri, *K. Miyabe & Y. Tokubuchi in 1890* (SAP, TI); Sapporo, *K. Miyabe in 1891* (GH, MO); Ishikari, Sorachibuto, Sorachi, *K. Miyabe in 1891* (PH, SAP, TI); Iburi, Chitose, *K. Miyabe & S. Arimoto in 1902* (SAP); Mt. Moiwa, *M. Mizushima in 1943* (TI); Sapporo city, Mt. Maruyama, *M. Mizushima 2604* (TI); Oshima, Mt. Sengen-dake, *K. Munakata in 1960* (MASS, MHA, MO); Ishikari, Nopporo, *G. Murata 8996* (KYO); Yubari city, *Y. Murata in 1952* (KANA); Mt. Moiwa, *T. Nakai in 1920* (TI); Mt. Apoi, *T. Nakai in 1928* (TI); Ishikari, Nopporo-genshurin, Nishi-nopporo, Ebetsu-shi, *N. Naruhashi 1139* (H, K, MAK, SHIN, TI, TNS, UC); Kitami, Mombetsu-gun, Takino-ue-mura, *S. Okamoto in 1950* (KYO); Kushiro, Mt. Shironuka, *S. Okamoto 584* (KYO); Tokachi, Shibetsu, Shikaoi, *S. Okamoto in 1955* (KYO); Mt. Shiratori, *S. Okamoto 1519* (KYO); Okushibetsu, *S. Okamoto 1811* (KYO); Kamiiso-gun, Kamiiso-cho, Hekirichi-gawa R., *T. Shimizu 0937* (KYO); Hidaka, Saru-gun, Tomikawa, *Y. Takahashi in 1963* (SAP); Sapporo, *Takenobu in 1880* (SAP); Teshio Experimental Forest, Minoshima-goe, *M. Tatewaki in 1928* (SAP); Notapu, *Y. Tokubuchi in 1888* (SAP); Hidaka, Samani, *Y. Tokubuchi in 1892* (SAP); Hidaka, Horoizumi, *Y. Tokubuchi in 1892* (SAP); Ishikari, Uashinai Coal Mine, *Y. Tokubuchi in 1892* (SAP); Hidaka, Saruru-mura, *Y. Tokubuchi in 1892* (SAP); Iburi, Chitose-gun, Aosari, *Y. Tokubuchi in 1893* (SAP, UC); Shiribeshi, Mt. Karibu, *I. Yamamoto in 1923* (SAP); Oshima, Mt. Gusin, *I. Yamamoto in 1925* (SAP); Oshima, Gampiyama, *I. Yamamoto 675* (SAP, TAI); Ishikari, Mt. Tengu, *I. Yamamoto 3752* (SAP); Iburi, Tanibujigawa, Date, *I. Yamamoto 9258* (KYO); Kitami, Sanrubeshibe, Nayoro, *S. Yokoyama in 1892* (SAP); Okawa, Keimagaichi, *S. Yokoyama in 1937* (SAP); Shiribeshi, Okushiri Island, *B. Yoshimura in 1935* (SAP); Konuma-hen, *without collector in 1878* (TI); near Sapporo city, Onuma, *without collector in 1878* (TI); Lake Toya-ko, *without collector* (MAK 117719). HONSHU: AICHI PREFECTURE: Kitashidara-gun, Nagura, *U.*

Matsuzaki in 1911 (MAK); Mt. Dando, *G. Murata 6520* (KYO). AKITA PREFECTURE: Kita-akita-gun, Mt. Moriyoshi, *H. Hara in 1959* (TI); Yamamoto-gun, Hibiki-mura, Nibuna, *T. Makino in 1927* (MAK 6944, S); Oja Peninsula, Motoyama, *R. Mochizuki 2236* (KANA); Mt. Moriyoshi-yama, Nakamura to the summit, *H. Ohashi 4852* (TI); Lake Tazawa-ko, *I. Yamazuta 36* (MAK). AOMORI PREFECTURE: Noeiji, mts. of Koiboshi, *U. Faurie 983* (MO, P); Aomori, *U. Faurie 5096* (KYO); Higashi-tsugaru-gun, Tairadate-mura, Yunosawa, *H. Hara in 1959* (TI); Aomori city, Kouhata, *K. Hosoi in 1950* (TNS); Mt. Hakkoda, Jougakura, *K. Hosoi in 1950* (KANA, TNS); Shimokita-gun, Ohata-cho, *K. Hosoi in 1951* (KANA); Mt. Hakkoda, Tsuta, *A. Kimura et al. in 1955* (TUS); Mt. Hakkoda, *H. Koriba s.n.* (TI); Mt. Osoro-san, Shimokita Peninsula, *O. Mori in 1959* (MAK); Shimokita-gun, Saimura, *O. Mori 14312* (S); Mt. Hakkoda, Sukayu to Shinyu to Jogakura, *H. Ohashi 68731* (MAK, TI); Masukawa, Miyama-mura, Minami-tsugaru-gun, *S. Okamoto in 1963* (KYO); Shimokita Peninsula, Osore-yama-yagen, *K. Yoshioka & K. Sugawara in 1964* (TUS). CHIBA PREFECTURE: Mt. Kiyosumi-yama, *S. Asano in 1932* (TNS). FUKUI PREFECTURE: Oono city, from Katugayu to Karikomi-ike, *N. Fukuoka & Y. Inamasu 423* (KYO); Ono-gun, Itoshiro, *G. Masamune 9248* (KANA); Nada-no-sho-mura, *Watanabe in 1965* (KYO), FUKUSHIMA PREFECTURE: Yama-gun, Nishiadzu-cho, S foot of Mt. Iide, *D. E. Boufford & E. W. Wood 19081* (MO); Mt. Futamata, *R. Endo in 1913* (TUS); Nishishirakawa-gun, *N. Imai in 1907* (MAK); Asaka-gun, Tadano-mura, from Yamada-hara to Mitsumori Pass, *H. Hara & S. Kurosawa in 1957* (TI); from Ozenuma to Ozegahara, Shimotashiro, *M. Mizushima 10443* (TI); Minamiaizu-gun, Oze, *G. Nakahara in 1904* (TNS); Minamiaizu-gun, Kotsunagi Pass, *J. Ohwi & M. Tagawa 597* (KYO); Nishishirakawa-gun, Kamaiyama-mura, *D. Shimizu in 1907* (MAK); Nishishirakawa-gun, Kanayama-mura, *D. Suzuki in 1906* (MAK); Mt. Iide, *without collector in 1907* (MAK 117735); Minamiaizu-gun, Numayama Pass, *without collector in 1916* (MAK 117732). GIFU PREFECTURE: Norikura, *U. Faurie 6681* (KYO); Yoshishiro-gun, Miyagawa-mura, *H. Furuike 8325* (KANA); Gunjo-gun, Okuakita-mura, Mizusawa-ue, *H. Kankebo 8092* (KANA): Kijo-gun, Mamba, *N. Satomi in 1961* (KYO); Hakuno village, *K. Shiota in 1923* (KYO); Yoshiki-gun, Miyakawa-mura, from Utsubo to Mannami, *N. Yonezawa 340, 488* (KANA). GUNMA PREFECTURE: Mt. Myogi, Kitakamura-gun, Myogi-machi, Hakuun-zan, *M. Furuse in 1957* (A, KAG, S); Kotsuke, Kouzubokujou, *K. Hiyama 1731* (TNS); Minamimaki-mura, Tsukigata, *N. Ishii 2* (TNS); Tone-gun, Minakami-cho, Mt. Tanigawa-dake, *H. Kanai 4446* (TI); Tone-gun, near Doai, *H. Kanai 4516* (TI); between Tokura & Yamanohana, *S. Kitamura in 1952* (KYO); Tone-gun, Minakami-cho, NE foot of Mt. Tanigawa-dake, *H. Koyama 5525* (KYO, MO); Usui-gun, Hakuunzan in Mt. Myogi-san, *G. Murata 27439* (KYO); Mt. Akagi-san, beside Lake Onuma, *M. Nishida 628* (E, TI); Yubiso, Nishikurosawa, *R. Noguchi in 1933* (TNS); Hanayashiki Spa, *J. Ohwi in 1929* (KYO); Tone-gun, Katashina-mura, from Tokura to Oze, *J. Ohwi & M. Tagawa 238, 244* (KYO); near Karizawa, *T. Saito in 1905* (MAK); Usui-gun, Matsuida-machi, Mt. Miyogi, *K. Satoh in 1954* (TI); Tone-gun, Mt. Omine, *T. Satomi 14460* (S); Azuma-gun, Tsumagoi village, *A. Takizawa 76* (SHIN); Tanigawadake, Yubiso-gawa R., *T. Yamazaki 619* (NCU, TI); Mt. Akani, Lake Akani, *without collector in 1916* (MAK 117730). HIROSHIMA PREFECTURE: Mt. Agatsuma, *W. Sato in 1932* (KANA); Hiba-gun, Otaki-dani, *K. Seto 22603* (OSA). HYOGO PREFECTURE: Yabu-gun, Sekinomiya-cho, NE foot of Mt. Hyonosen, *D. E. Boufford & E. W. Wood 19513* (BM, CM, DS, G, GH, K, KYO, LD, LE, MASS, MHA, MO, NCU, NY, P, PE, S, SHIN, UC); Mt. Hyonosen, *D. E. Boufford et al. 19566* (KYO, MO); Yabu-gun, Oya-cho, Ikada, *D. E. Boufford et al. 19574* (MO); N slope of Mt. Hachibuse, *D. E. Boufford et al. 19591* (BM, CAS, CM, G, GH, K, KYO, LD, MHA, MO, NCU, P, PE, S, SHIN, UC); Mikata-gun, Mt. Sugano-sen, *N. Fukuoka & Y. Inamasu 728* (KANA, KYO); Mt. Ogino-yama, *S. Hosomi 7237* (KYO); Urarokuko, Karatonotani, *E. Ishikawa in 1935* (TAI); Mikata-gun, Onsen-cho, Mt. Oogino-sen, *K. Iwatsuki 6576* (KYO); Mt. Myoken, *S. Kitamura & G. Murata 633* (KYO); Shiso-gun, Haga-cho, SE foot of Mt. Mimuro-yama, Akanishi-dani, *N. Kurosaki in 1976* (KANA); Kiritaki, Onsen-cho, Mikata-gun, *G. Murata 20680* (KYO, MAK); Mikata-gun, Onsen-cho, *G. Murata 20703* (KYO, TI); Mikata-gun, Onsen-cho, from Umigami to Ogino-sen, *G. Murata 20750* (KYO); Sayo-gun, Nanko-cho, Mt. Funakoshi-yama, *G. Murata 33786* (KYO, MO); Shiso-gun, Haga-cho, Tokura, *G. Murata 20363* (KYO); Yabu-gun, Oya-cho, Yokoyuki to Mt. Hyonosen, *G. Murata 22088* (KYO, TI); from Mt. Rokko to Arima, *M. Tagawa 6915* (KYO); Mt. Hino-san, *Y. Yoneda in 1932* (KYO). IBARAKI PREFECTURE: Mt. Tsukuba, *T. Makino s.n.* (MAK 6945); Tsukuba-gun, Mt. Tsukuba, *T. Makino in 1923* (MAK); Mt. Tsunuba, *H. Sakurai in 1911* (E); Mt. Tsukuba, *S. Tako in 1909* (MAK). ISHIKAWA PREFECTURE: Mt. Hakusan, Iwama Spa, *N. Fukuoka in 1961* (KYO); Hakusan, Iwama, *M. Hashimoto 4330* (KANA); Hakusan, *T. Ichimura 1442* (KANA); Hakusan, Ichinose, Shitsudo, *G. Masamune 7345* (KANA); Ishikawa-gun, Hakusan, Tyugu-michi, *G. Masamune 11666* (KANA); Ishikawa-gun, Iwame, *G. Masamune 11926* (KANA, SHIN); Ishikawa-gun, between Ichinose & Murodo, *G. Masamune 16366* (KANA); Kanagawa city, Yokotani-cho, *T. Nishimura in 1959* (KANA); Shiro-yama, *K. Shiota 2723* (GH); Hakusan, Iwama Hot Spring, *H. Sugino in 1956* (KANA); Karagokuman-san, *S. Tanaka in 1961* (KANA); Kanazawa city, Agaharai-yama, *S. Tanaka in 1963* (KANA). IWATE PREFECTURE: Mt. Hayachine, *U. Faurie 13593* (G, MO, P); Mt. Iwate, *M. Honda in 1927* (TI); Shimohei-gun, Ogunimura, Mt. Hayachine, *H. Kanai in 1959* (TI); Morioka city, Asagishi, *M. Kikuchi in 1967* (TNS);

Kunohe-gun, Hiraniwa-dake, *M. Miora in 1904* (SAP); Mt. Himekami, *K. Ogata 4056* (KAG); Mt. Hayachine, *Y. Ogura in 1915* (TI); Osawa in Miyako city, *H. Ohashi 9173* (A, FSU, TI); Mt. Iwate-san, *H. Sakurai in 1900* (TNS); Kamihei-gun, Goyo-zan, *S. Sasamura in 1954* (MAK). KANAGAWA PREFECTURE: Hakone, *Delessert in 1883* (G); Mt. Hakone, *M. Hiroe 5143* (KYO); Kurokura, *K. Hisauti in 1919* (LD); Mt. Oyama, *Iijima in 1887* (TNS); Hatano city, Mt. Tanzawa, near Shindainichi, *H. Kanai in 1952* (TI); Hafano city, Mt. Tanzawa, *H. Kanai in 1956* (TI); Mt. Tanzawa-yama, *S. Kiyoshi in 1960* (TNS); Hakone, Ashigarashimo-gun, *T. Makino in 1919* (MAK 6948, S); Hakone, Mt. Kozuka, *M. Mizushima in 1949* (TI); Mt. Hakone, shores of Lake Ashino-ko, *S. Okamoto in 1967* (KYO); Mt. Oyama, *S. Okuyama in 1958* (TNS); Yabitsu-toge, *T. Saito in 1963* (TNS); Hakone, Ashino-ko, *T. Sawada 2286* (E), *2287* (TI); Hakone, Kojiri, *T. Sawada 2289* (DAO, TI); Hakone Skyline, *J. Sugimoto in 1967* (TNS); Hakone, middle elevation of Mt. Kami-yama, *H. Yamamoto 2011* (TNS); Hakone, Otome Pass, *H. Yamamoto 2446* (TNS); Mt. Tanzawa, *T. Yamazaki 783* (K, TI). KYOTO PREFECTURE: Yosa-gun, Iwaka-mura, Mt. Taiko, *Y. Araki in 1932* (KYO); Kita-kuata-gun, *Y. Araki 367* (KYO); Kita-kuata-gun, Chi-mura, Experimental Forest of Kyoto Univ., *Y. Araki 476* (KYO); Mt. Hiei, *S. Hattori in 1926* (TI); Kyoto city, Sakyo-ku, Mt. Kurama, *M. Hiroe 18074* (UC); Ashiu, Chii-mura, *T. Horikawa & G. Nakai 5590* (KYO, SAP); Mt. Hiei, *S. Kawagoe 2092* (KAG); Mt. Hiei-zan, between Shimeigadake & Seiryuji, *G. Murata 11417, 13030* (KYO); N of Kyoto, Daihizan, *G. Murata 9906* (KYO); Ashiu, Chii-mura, *G. Nakai 5590* (MICH); Ashiu Experimental Forest of Kyoto Univ., *A. Nitta 12586* (KYO), *S. Okamoto in 1936* (KYO); Mt. Hiei, *M. Tagawa 285* (KYO); Kurameyama, *without collector in 1900* (MAK). MIE PREFECTURE: Mie-gun, Komono-machi, Mt. Kamaga-dake, Nagaishi-dani, *N. Fukuoka 4938* (KYO); Kameyama city, summit of Mt. Nonobori, *N. Fukuoka 5143* (KYO, SHIN); Ichishi-gun, Misugi-mura, Mt. Miune, Hirakura Experimental Forest, *N. Fukuoka 6052* (KYO); Mt. Hirakura, *S. Kitamura in 1963* (KYO); Ichishi-gun, Misugi-mura, Experimental Forest of Mie Univ., *G. Murata 18489* (KYO); Osugi-dani, *S. Okamoto in 1941* (TNS); Suzuka-gun, Mt. Nonobori, *T. Shimizu 4020* (KYO). MIYAGI PREFECTURE: Mt. Fubo-san, Namari-zawa, *D. E. Boufford & E. W. Wood 19873* (CM, KYO, MHA, MO, PE); Ebino to Eodani, *Honda in 1929* (KAG); Okunikkawa, *T. Ishida & Y. Hayashi in 1959* (KYO); Sendai, Aoba-yama, Tohoku Univ. Bot. Gard., *A. Kimura & K. Ohmiya in 1960* (TUS); Miyagi-cho, Okunikkawa, *C. Kimura in 1970* (TUS); Kinkasan Island, *C. Kimura in 1970* (TUS); between Sone & Gaga, *A. Kimura & S. Sugaya in 1950* (TUS); Mt. Zao, *A. Kimura & S. Sugaya in 1953* (TUS); Natori-gun, Okunikkawa, *H. Ohashi 9993* (TI); Gaga Hot Spring, *S. Okayama 9319* (TNS); Kinka-san Island, *S. Sugaya & T. Fujita in 1955* (TUS); Mt. Kurikoma, *S. Sugaya et al. in 1952* (TUS); Mt. Kinka-zan, *Z. Tashiro in 1935* (KYO). NAGANO PREFECTURE: base of Mt. Norikura, *U. Faurie 6681* (BM, G, KYO, P, W); Karuizawa, Sentinel Rock, *H. E. Fox in 1912* (BM); Nakabusa-onsen, *H. Fujimori 172* (SHIN); Shimoina-gun, Ikuta-mura, *M. Fukuyo 75* (TNS); Shimoina-gun, Ikuta-mura, Kayarama, *M. Fukuyo 131* (TNS); Shimoina-gun, Oshika-mura, *H. Furuike in 1956* (KANA); Shimoina-gun, Tatsuoka-mura, *I. Furusawa in 1940* (TI); Shimoina-gun, Oshika-mura, from Fukasawa to Tsubame-iwa, *I. Furusawa in 1940* (TI); Minami-azumi-gun, Mt. Jyonen-dake, *I. Furusawa in 1941* (TI); Karuizawa, *F. C. Greatrex K52/30* (TI); Shimashima, *S. Hattori in 1925* (TI); Togakushi-mura, *H. Ichio in 1966* (KANA); Kamiminochi-gun, Kinasa-mura, Okususubana, *S. Ito 192* (SHIN); Mt. Nomugi-toge, *T. Ito in 1891* (TNS); Shimoina-gun, Ooshika-mura, from Kamazawa to Koshibuyu, *K. Iwatsuki & H. Koyama 33* (KYO, TNS); Shimoina-gun, Ooshika-mura, from Koshibuyu to Hirogawara, *K. Iwatsuki & H. Koyama 69* (KYO, TNS); Nishi-chikuma-gun, Todachi-mura, Todachi-taki, *H. Kanai in 1957* (TI); Suwa city, between Kirigamine & Yashima, *S. Kobayashi in 1960* (CAS, MAK); Kiso, Mt. Ontake, *G. Koidzumi in 1910* (TI); Oshika-mura, Kamasawa, *S. Kuraishi in 1953* (TI); Taira-mura, Ohmachi city, Otsumetasawa, *S. Mimoro & S. Tsugaru 987* (KYO); foot of Mt. Asama, from Kose to Shiraito-no-taki, *M. Mizushima in 1951* (TI); Tobira-toge, *S. Momose in 1933* (TI); Shimoina-gun, Igara-mura, Yomogidaira, *M. Muramatsu 648* (TNS); Kamiina-gun, Ooshika-mura, Mt. Odaka-yama, *M. Muramatsu 1512* (TNS); Shimoina-gun, Kizawa-mura, Nishisawado, *M. Muramatsu 2642* (TNS); Shimoina-gun, Kizawa-mura, Iroudo, *M. Muramatsu 3473* (TNS); Togakushi-mura, *G. Murata 6413* (KYO); Nishichikuma-gun, Nagiso-cho, Shizumo Government Forest, *G. Murata et al. 142* (KYO); Yatsuga-dake, *T. Naito 6770/14330* (KAG); Mt. Togakushi, *Y. Nakajima in 1913* (TUS); Sasagamine, from Bokujo to Mt. Kuromime, *A. Nitta 11714* (KYO); Tokugo Pass, *Y. Ogura in 1917* (TI); Mt. Komaga-dake, *T. Saiki in 1910* (MAK); Mt. Togakushi, *H. Sakurai in 1898* (TNS); Mt. Arafune, *K. Sato 178* (TI); Nakagomi-cho, Uchiyama, Mt. Arafune, *K. Sato 324* (TI); Chiisata-gun, Sugadaira, along Daimyo-jinzawa, *T. Shimizu 18996* (SHIN); Yokokawa-dani valley, Okaya, *T. Shimizu 25803* (SHIN); Suwa-gun, Fujimi-cho, Shirakawa valley, *T. Shimizu 25870* (SHIN); Nishi-chikuma-gun, Shinkai-mura, Experimental Forest of Kisosanrin High School, *Y. Shirai 57* (SHIN); Kitasaku-gun, Karuizawa, Usui-toge, *Y. Tateishi 1333* (TI); Shimoina-gun, Oshika-mura, Shiokawa, *K. Teramoto in 1947* (TI); Shimoina-gun, Kisawa-mura, Toyama-gawa R., *Yamasaki et al. in 1954* (TI); Mt. Ontake, *R. Yatabe in 1880* (BM); Kita-azumi-gun, Mt. Hakuba, *T. Yazawa in 1903* (SAP); Takeishi Pass, *without collector in 1931* (TI). NARA PREFECTURE: Mt. Omine, *K. Adachi in 1910* (MAK); Yoshino-gun, Tenkawa-mura, from Dorogawa to Houriki-toge, *N. Fukuoka & M. Hotta 6*

(KANA, KYO); Yoshino-gun, Tenkawa-mura, Mt. Imine, between Chosen-dake & Tsubonouchi, *N. Fukuoka & M. Hotta 271* (KYO); Yoshino-gun, Mt. Shakaga-take, *M. Hiroe 18226* (KYO, UC); Mt. Omine, *S. Kitamura in 1950* (KYO); Mt. Wasanata-yama, *T. Kodama 10824* (OSA); Mt. Kasasute-yama, *G. Koidzumi in 1922* (KYO); Mt. Odaigahara, *G. Koidzumi in 1922* (KYO); Odaigahara-yama, Goshiki-yu, *G. Nakai 3476* (KYO); Yoshino-gun, Mt. Odaigahara, *H. Nishimura 485* (KAG, KYO, TNS); Omine Mts., Yoshino-gun, from Mt. Misen to Gyogaeri, *T. Shimizu 4304* (KYO). NIIGATA PREFECTURE: Mt. Kurohime, *T. Ajima 4312* (KANA); Kitauonuma-gun, Okutadami Lake, Nakanomata, *H. Kanai et al. 8910* (TI); Nakauonuma-gun, Yuzawa, *S. Kobayashi 15142* (S); Mt. Mioko, *S. Matsuda in 1894* (KYO); Kitauonuma-gun, Irihirose-mura, Mt. Asakusa, *T. Yamazaki 6534* (TI); Itoigawa city, Mt. Nyogo, *T. Yasushima in 1976* (KANA); Mt. Shimizu-toge, *without collector in 1886* (K); Kitauonum-gun, Gin-zan-daira, *without collector in 1908* (MAK); Tazawa-mura, *without collector in 1931* (TI). OKAYAMA PREFECTURE: Hideta-gun, Mimasaka, *S. Arimoto in 1903* (SAP); Ushiroyama, *S. Arimoto in 1903* (GH); Okayama, *T. Makino in 1906* (MAK). OSAKA PREFECTURE: Minamikawachi-gun, Mt. Kongo, *T. Makino in 1927* (DAO, KAG, KYO, MAK 6949, TI); Minamikochi-gun, Chihaya-akasaka village, Mt. Kongo, *S. Mimuro et al. 10439* (KYO); Mt. Kongo-san, from Chihaya to Fushimi-toge, *G. Murata 27049* (KYO, US); Mt. Kongo-san, *M. Tagawa 3354* (KYO). SAITAMA PREFECTURE: Chichibu-gun, Ryoogami-mura, Mt. Futago, *H. Hara & S. Kurosawa in 1957* (TI); Tanzawa, Genmo-kura, *K. Hisauchi 1641* (TI); Chichibu, *T. Naito s.n.* (KAG); Musashi, Mt. Izugatake, *S. Okuyama in 1935* (TNS); Chichibu-gun, Mt. Mitsumine, *F. Sakaguchi in 1906* (MAK); Chichibu, Kawaishi-mura, *H. Sakurai in 1892* (TNS); Mt. Buko, *S. Tanaka in 1963* (KANA). SHIGA PREFECTURE: Gamou-gun, Ichihara-mura, Chikusa-goe, *C. Hashimoto 1506* (TNS); Inukami-gun, Oikedani, N of Oike-dake, *H. Koyama & N. Fukuoka 28* (SHIN); Mt. Ibuki, *T. Makino in 1906* (MAK); Mudoji-dani, Mt. Hiei-zan, *G. Murata 20265* (KYO); Gamo-gun, Nishioji village, *G. Nakai 4693* (KYO); Ohmi, Mt. Hiei-zan, *without collector in 1908* (TNS 16172). SHIMANE PREFECTURE: Sahime-mura, Mt. Sanbei-yama, *G. Murata 11708* (KYO); Mt. Senzu, *T. Naito in 1927* (KAG). SHIZUOKA PREFECTURE: Akaishi Mts., Koshibu-gawa, *Furusawa & Kuraishi in 1953* (TI); Mt. Hakkozan, *G. Hashimoto in 1933* (TNS); Miyake Island, *Hayashi in 1936* (KYO); Mt. Fuji, Kamitake-yama, *B. Hayata in 1924* (TI); Skyline Hiking Course between Nakko Pass & Amagi Pass, *M. Hotta 6117* (KYO); Aitaka Mts., from Suyama to Kurotake, *H. Kanai 5826* (TI); Aitaka Mts., from Yanagisawa to Aitakasan, *H. Kanai 5828* (TI); Aitaka Mts., Echizen-dake, near Fujimi-dai, *H. Kanai 5832* (TI); Aitaka Mts., Nokogiri-dake, *H. Kanai 5833* (TI); Aitaka Mts., Motosawa, *H. Kanai 7233, 7345* (TI); Umegashima, *S. Kitamura in 1966* (KYO); Nakamata, *S. Mashiko in 1954* (KAG); Mt. Amagi, *S. Matsuda in 1899* (KYO); Ohwigawa-joryu, Tokusa, *S. Matsuda in 1954* (TI); Kitamuro-gun, between Chihiro Pass & Funatsu, *G. Murata 10192, 10201* (KYO); Abe-gun, Umegashima-mura, Ootaki, *G. Murata et al. 214* (KYO, SHIN); Mt. Amagi, *T. Nakai in 1931* (TI); Mt. Kintoki to Mt. Ashigara, *H. Noguchi 4850* (KAG); Mt. Amagi, *H. Noguchi 6381* (KAG); Seto-no-tani, Utoge-no-taki, *D. Shimizu in 1930* (TI); Mt. Fuji, Subashiri, *M. Takeuchi in 1948* (TI); Mt. Fuji, Suruga, *without collector in 1879* (TNS 8715). TOCHIGI PREFECTURE: Nikko, Umagayeshi, *J. Bisset 4206* (BM, E); foot of Mt. Nantai-san, *S. J. Enander in 1913* (S); Nikko, *M. Furuse in 1954* (A); Nikko, from Chuzenji to Shobugatake, *M. Honda in 1924* (TI); Nikko, *T. Ichimura 1438* (KANA); Kirifuri, *H. Ito in 1931* (TI); Nikko city, Nikko, *T. Makino in 1903* (MAK, S, TUR); Nikko, Urami-taki, *M. Mizushima in 1946* (KANA); Nikko, near Jakko-no-taki, *J. Murata & H. Ohashi in 1975* (KYO, TI); Nasu, from Santogoya-onsen to Ootoge, *G. Murata 18217* (KYO); Katashina-mura, from Oshimizu to Mihira Pass, *M. Nishida in 1950* (TI); Ose, *J. Ohwi & M. Tagawa 238* (UPS); Shioya-gun, Kuriyama-mura, *S. Sugaya in 1934* (TUS); near Oonuma, Oku-shiobara, *S. Suzuki in 1951* (UC, WTU); Kamitsuga-gun, Furumine Shrine, *D. Suzuki in 1906* (MAK); middle elevation of Mt. Koshin-zan, *M. Tagawa & K. Iwatsuki in 1957* (KYO); Nikko, *H. Takeda 254* (K), *T. Uno 254* (BM); Mt. Tanigawa-dake, Tanigawa-mototani, *T. Yamazaki in 1948* (TI). TOKYO PREFECTURE: Mt. Takao, *S. Hattori in 1922* (TI); Motohachioji, *K. Hisauti s.n.* (LD); Mt. Takao, *K. Hisauti 1640* (LD, TI); Mt. Ryogami, *K. Hisauti in 1942* (MT); Mt. Takao, *K. Hiyama in 1929* (TNS); Nishitama-gun, Asakawa, Mt. Takao, *H. Kanai in 1954* (TI); Asakawa, Koshita-sawa, *H. Kanai 298* (TI); Nishitama-gun, Nippara, Kurasawa, *H. Kanai 4234* (TI); Nishitama-gun, Mt. Mitake-manayo Falls, *S. Kobayashi 1049* (CAS); Mt. Omae, *H. Mizushima in 1946* (TI); Nishitama-gun, Mt. Minoto, *M. Mizushima 10034* (UC); Shiro-yama, *S. Okuyama in 1934* (TNS); Kamagoke-gawa, *H. Ono in 1948* (TI); Shiro-yama, *T. Sato in 1934* (TNS); Omue city, Kaminari-gi, *T. Satow 8733a* (KYO); Akikawa, *T. Satow 8895* (KYO); Mt. Takao, *S. Suzuki in 1951* (UC, WTU); Okuchichibu, Deosing-san, *M. Tagawa in 1930* (KYO); Nishitama-gun, Mt. Mitake, *M. Tsunaki 3251* (TI); Kawanori-yama, *T. Yamazaki & H. Ono in 1948* (TI); Nishitama-gun, Mt. Takamizu-san, *T. Yamazaki 2602* (TI); Nishitama-gun, Gozen-yama, *T. Yamazaki 2282* (TI); Tokyo-teishitsu, *without further data* (TNS 13227). TOTTORI PREFECTURE: Daisen, from Masumizuhara to Miyama, *M. Hashimoto 3815* (KANA); Saihaku-gun, Kabuto R., *A. Tanaka 15871* (KYO); Yazu-gun, Wakazakura town, Mt. Hino-san, *A. Tanaka 12878* (KYO). TOYAMA PREFECTURE: Tateyama-machi, Midaga-hara, *L. Charette 1970* (MO); Tateyama, *T. Ichimura 1437* (KANA); Shimoshinkawa-gun, Asahi-machi, near Ogawa Hot Spring, *H. Kanai in 1958* (TI), *H. Kankeko in 1962*

(KANA); Nei-gun, Yamada-mura, Mt. Ushigatake, *A. Kirino 788* (COLO, S, TNS); Shinkawa-gun, Kamiichi-machi, Kamaike, *N. Kurosaki 2140* (KYO), *2141* (KANA, TNS); along Katagai-gawa, Uozushi, *K. Nagai in 1969* (KYO); Kurobe, Kanetsuri-onsen, *J. Ohwi 7305* (KYO), *S. Okamoto in 1935* (KYO); Mt. Ioo, Nakane-Yokotani Pass, *S. Ooura in 1961* (KYO); Wada R., *without collector in 1907* (MAK 6936). WAKAYAMA PREFECTURE: Minamikawachi-gun, Mt. Kongo, *T. Makino in 1927* (S); Nishimuro-gun, Ooto-mura, Wada R., *G. Murata & F. Konta 72* (KYO), *175* (KYO, MAK, TI); Hidaka-gun, Naotsuma-mura, Kawamata, *T. Nakashima in 1929* (KYO, TI); Hidaka-gun, Kawakami-mura, Seo, *T. Nakashima in 1931* (TI); Hidaka-gun, Ryujin-mura, Nanogakiuchi, *T. Nakashima in 1931* (TI); Mt. Koya, *Y. Ogawa in 1956* (KANA); Kumano-gawa-cho, Oguchi, *Y. Ogawa in 1959* (KANA); Arita-gun, Yawata-mura, *S. Okamoto 19428* (TI); Experimental Forest, *K. Sato 22882* (SAP); Gonzui-Kubotani, Wakayama Experimental Forest, *M. Tatewaki in 1930* (SAP); Higashi-muro-gun, Mitsukoshi-toge, *without collector in 1883* (TI); Mt. Koyasa, *without collector in 1912* (MAK). YAMAGATA PREFECTURE: *W. R. Carles in 1895* (E); Mt. Asahi, Nekogawa, Higare-goya, *H. Hara in 1959* (TI); Mt. Asahi-dake, Kodera-kosen, *H. Hara in 1959* (TI); Nishimurayama-gun, Asahi-cho, from Kikawa to Asahi Kosen, *K. Iwatsuki et al. 578* (KAG, KYO, SHIN, TNS); Oguni, *C. Kimura & T. Moruma in 1966* (TUS); Higashitagawa-gun, Uenagawa-mura, *K. Mori in 1931* (KANA); Ootori-mura, *T. Nagasawa in 1891* (TNS); between Yamdera & Futakuchi Pass, *H. Ohashi in 1960* (TUS); Kabuto-iwa, in Okuyamadera, *H. Ohashi 2548* (TI); Yamagata city, near Kabutoiwa, *H. Ohba 718033* (H); from Chojabara to Otamagawa, *M. Ono in 1954* (TI); Mt. Iide near Haraikawa, T. Yamazaki in 1943 (TI); foot of Mt. Azuma-san, *Yoshida in 1915* (MAK). YAMAGUCHI PREFECTURE: Suwo, Kuko-gun, Mt. Jakuchi, *J. Nikai in 1920* (TNS); Mt. Kanchi, *Z. Tahiro s.n.* (KYO). YAMANASHI PREFECTURE: Ensan city, from Daibusatsurei to Sakeishi, *N. Fukuoka 5053* (KANA); Unoshima, *K. Hiyama 6910* (TNS); foot of Mt. Koma, *S. Kitamura in 1931* (KYO); Minamitsuru-gun, Mt. Fuji, Komitake, *S. Kobayashi 1468* (CAS); Minamikuma-gun, Tentsuki Pass, *Matsuda & Fujita in 1954* (TI); Mt. Fuji, Kurotsuka, *H. Muramatsu in 1927* (TI); Kozuke-hara town, Gun-nai, *S. Okamoto in 1935* (KYO); Kiosato, foot of Mt. Yatsuna-dake, *M. Ono in 1964* (MAK); Ashi-hara-mura, Mt. Kitadake, vicinity of Hirogawara, *H. Tamura & M. Hotta 3742* (KYO); Daibosatsu-mine, *H. Uematsu in 1949* (TI); Nakakoma-gun, Ashiyasu-mura, *T. Yamazaki in 1954* (TI). KYUSHU: FUKUOKA PREFECTURE: Tagawa-gun, Soeda-cho, Mt. Hiko, *T. Hashimoto in 1952* (TI); Mt. Shaka-dake, *S. Masamura 14* (KAG). KAGOSHIMA PREFECTURE: Kirishima, *H. Asuyama in 1929* (TNS); Mt. Kirishima, Takachihogawara, *S. Hatusima 26175* (KAG); Mt. Higashi-kirishima, *Z. Tashiro in 1919* (KYO). KUMAMOTO PREFECTURE: Mt. Ichifu-san, *S. Hatusima 14161* (KAG); Gokanosho, Mominoki, *S. Hatusima 15023* (KAG); Mt. Karimata-yama, Nihonsugi, Gokanosho, *S. Hatusima 27799* (KAG); Matashidani, Gokanosho, *S. Hatusima 31943* (KAG); Shakain, *M. Kozuma in 1933* (TNS); Momiki, Gokanosho, *S. Sako 997* (KAG); Mt. Kamifukune, Gokanosho, *S. Sako 1197* (KAG); Yatsushiro-gun, Nasugoe, *Z. Tashiro in 1915* (TNS). MIYAZAKI PREFECTURE: Nishiusuki-gun, Hinokage-cho, from Kamikawa to Mt. Doo-dake, *N. Fujita 156* (KANA, KYO); Mt. Kirishima, Ebino, *S. Hatusima 15126* (KAG); Hori & Mt. Okue, *S. Hatusima & S. Sako 25179* (KAG, KYO); Mt. Wanizuka, *S. Hatusima 32654* (KAG); Koyu-gun, Kijiro-mura, Mt. Osuzu, *I. Hurusawa in 1949* (TI); Higashi-usuki-gun, Togo-mura, from Tabuki to Mt. Osuzu, *H. Kanai in 1958* (TI); Higashiusuki-gun, Shiiba-mura, near Nakayama, *H. Kanai in 1958* (TI); Mt. Kirishima, *H. Otagawawachi s.n.* (KAG); Kitamorogata-gun, Ushitoge, *S. Tanaka in 1890* (TNS); Osuzuyama, Tuno-machi, *S. Yosie in 1936* (TI). NAGASAKI PREFECTURE: Mt. Onsen-dake, *Kozuma & Masayuki 31234* (TNS); Nagasaki, *C. Maximowicz in 1863* (GH). OITA PREFECTURE: Mt. Kuju, *S. Hatusima in 1952* (KAG), *S. Sako 2789* (KAG); Kuju Range, Mt. Waita-zan, *M. Sato 2810* (KAG); Yabakei, *M. Togashi in 1961* (TI); Yufuin, *M. Togashi 7295* (TI). SHIKOKU: EHIME PREFECTURE: Iyo, Tsuchigoya, *H. Asuyama in 1931* (TNS); Niihama city, Sasagamine, *T. Ishikawa 42* (KYO); Uajima city, Mt. Oniga-jo, *M. Kono in 1907* (MAK); Kami-ukena-gun, Odamiyama, *Y. Momiyama 0-39* (TI); Mt. Ishizuchi, *T. Takatsu in 1971* (KANA); Uajima city, Nametoko, *Uemura in 1896* (MAK); Mt. Tamatatsuri, *M. Yamanaka in 1953* (TUS); Mt. Ishizuchi, *without collector in 1905* (MAK). KOCHI PREFECTURE: Aki-gun, Umaji, *I. Doi in 1901* (MAK); Mt. Yanase-yama, *S. Hatusima 22027* (KAG, MAK); Nagaoka-gun, Mt. Kuishi-yama, *G. Murata 10805* (KYO); Takaoka-gun, Honokawa, *S. Okamura in 1904* (MAK); Bokunokawa, Chio valley, *S. Okamura 35* (MAK); Aki-gun, Nishikawa, *N. Satomi in 1954* (KANA); Aki-gun, Yanase, Nishikawa, *N. Satomi in 1956* (KAG, MAK, S); Nagaoka-gun, Mt. Kajigamori, *K. Seto 2804* (OSA); Mt. Yokogura, *Z. Tashiro in 1901* (KYO); Yanase, *Y. Ueda in 1905* (MAK); Nanokawa, *K. Watanabe? in 1892* (K, US); Mt. Tebako, *S. Yano in 1890* (TI). TOKUSHIMA PREFECTURE: Mt. Takaetsu, *T. Kasai in 1912* (MAK); Miyoshi-gun, Higashi-yayama-mura, Ochiai, *G. Murata 7778* (KYO); Naka-gun, Shio-tani-mura, *G. Nakai 4132* (KYO); Mt. Tsurugi, *J. Nikai 1976* (TNS), *S. Nishima 1976* (TI), *H. Toyoshima in 1954* (TNS).

KOREA, SOUTH. Cheju-do ("Quelpaert Island"), *I. C. Chung 3900* (MICH); Zenranan-do, Mt. Hakuun-san, *S. Hohzawa in 1934* (TNS); Zenranan-do, Mt. Chii-san, *S. Hohzawa in 1937* (TNS);

Mt. Chii ("Mt. Tii"), *S. Okamoto 17933* (KYO); Cheju-do ("Quelpaert Island"), *E. Taquet 827* (G, LE), *without collector 1487* (KYO), *without collector 5177* (MICH).

Along with *Circaea cordata*, *C. erubescens* is one of the two most distinctive species of *Circaea*. The shallowly notched, obtrullate petals are unique in the genus. The presence of an exserted nectar-secreting disc; relatively long pedicels in flower and fruit; obovoid non-sulcate fruits; slender, purple sepals; conspicuously reddish-purple, somewhat shining nodes in life; and distinctive petals make *C. erubescens* easily recognizable. Except for the uncinate hairs on the ovaries, *C. erubescens* is usually glabrous throughout but some populations from Japan and from Cheju-do (Quelpaert Island), South Korea, may have the stem more or less densely pubescent with very short, almost dust-like, falcately recurved hairs. Most plants of *C. erubescens* have a somewhat spindly appearance and the usually numerous racemes, instead of being straight and erect as in other species, often diverge in various directions in relation to each other or may even project at right angles to the central axis of the plant. Often, in contrast to other species where the racemes are more or less equal in length on a single plant, the raceme branches in *C. erubescens* may be very unequal in length on the same plant.

Plants of *Circaea erubescens* from the western part of the range tend to have the leaves more consistently broadly ovate and less often lanceolate than plants from the central and eastern parts of the range. These western plants resemble *C. glabrescens* vegetatively and have been confused with that species in the past. *Circaea glabrescens* always has the nectary wholly included within the floral tube, petals wider than long, and the apical notch 0.3 mm or more long, generally pubescent buds, and generally shorter pedicels in both flower and fruit. *Circaea glabrescens* also has the stem pubescent while *C. erubescens* has glabrous stems in the regions where the two species overlap.

Circaea erubescens exhibits a greater range of ecological tolerance than other species of the genus. It is found in rocky or stony soils at the margins of streams, in moist alluvial forests, in fine soils, and on steep, often well drained slopes in upland areas in diverse soil types. This wide ecological amplitude allows *C. erubescens* to come in direct contact with a large number of other species and no doubt accounts for the greater number of known hybrids involving *C. erubescens* than any other species. *Circaea erubescens* is known to hybridize with *C. alpina* subsp. *alpina*, *C. cordata*, *C. lutetiana* subsp. *quadrisulcata*, and *C. mollis*. Additional hybrids between *C. erubescens* and *C. alpina* subsp. *caulescens* should be sought in Japan and in eastern China where the two come in contact, between *C. erubescens* and *C. alpina* subsp. *imaicola* in Taiwan and in southwestern China, between *C. erubescens* and *C. repens* in southwestern China, although it is not certain at the present time whether these latter two species come into direct contact, and between *C. erubescens* and *C. glabrescens* in central China. The ranges of *C. erubescens* and *C. repens* overlap only in a small area in southwestern China and the two species may be isolated altitudinally. Still, this should not preclude the possibility that hybrids may have been formed in the past. Raven (1963) has suggested that the widespread occurrence of *C.* × *intermedia* (*C. alpina* subsp. *alpina* × *C. lutetiana* subsp. *lutetiana*) outside of the range of one or both of the parents in the British Isles may be due to the

vegetative persistence of the hybrids from past times when climates were favorable for the two parents to grow together and hybridize.

6. Circaea repens Wallich ex Asch. & Magnus, Bot. Zeitung (Berlin) 28: 761. 1870.—FIG. 16.

Circaea repens Wallich, Numer. list, no. 6341. Nom. nud.

Circaea lutetiana sensu C. B. Clarke, in J. D. Hooker, Fl. Brit. India 2: 589. 1879; non Linnaeus, 1753.

Circaea alpina L. var. *himalaica* C. B. Clarke, in J. D. Hooker, Fl. Brit. India 2: 589. 1879. TYPE: Nepal, Gosainthan, 1824, *N. Wallich 6342* (K, lectotype; E, 2 sheets; G, 2 sheets; K, 2 sheets, isolectotypes; BM, LIV, probable isolectotypes).

Erect or occasionally decumbent at the base, 1.5–10 dm tall, simple or very rarely branched below the inflorescence; forming filiform rhizomes, each producing late in the season a tuberous thickening at the apex, the tubers giving rise to the following year's plants from their apices and to the following year's rhizomes from their nodes. Plants pubescent; the stem with soft, short, falcately recurved hairs, 0.2–0.3 mm long; the axis of the inflorescence and pedicels with capitate and clavate-tipped glandular hairs, 0.2–0.3 mm long, these merging with and giving way to the recurved hairs of the stem at the base of the inflorescence; the petioles with upwardly curved, falcate hairs, 0.2–0.3 mm long, these continuing along the main veins of the leaf on both surfaces, both surfaces of the leaf also with straight or slightly curved hairs, 0.3–0.5 mm long, these more numerous along the veins. Stem green, rarely reddish, the nodes brown, axis of the inflorescence green or somewhat purple. Leaves horizontally spreading, deep green or green, opaque, those just above the middle of the stem the largest, (1.8–)3–7(–9) cm long, (1.5–)2.5–5 cm wide, becoming gradually reduced in size upward and eventually bractlike and opposite, or the uppermost alternate, in the lower part of the inflorescence, gradually to abruptly reduced in size downward; narrowly to broadly ovate, rarely nearly orbicular, acute to short acuminate at the apex, broadly cuneate to cordate but more commonly rounded at the base, minutely to prominently denticulate. Petioles 1–5.5 cm long, with or without greatly reduced branches arising in the axils. Inflorescence pubescent, often densely so, with short, glandular hairs 0.2–0.3 mm long, and occasionally with a few, sharp pointed, patent hairs, 0.3–0.5 mm long, intermixed; a simple terminal raceme or, more commonly, the terminal raceme branched at the base and with secondary, simple racemes at the tips of the uppermost, reduced branches, when branched, the lateral branches alternate, rarely opposite, subtended by reduced leaves or leaflike bracts. The terminal raceme, from the uppermost reduced leaf or leaflike bract, 1.5–2 cm long at initiation of flowering, to 20 cm long at cessation of flowering; the lateral racemes ca. 2 cm long at initiation of flowering, to 18 cm long at cessation of flowering, subequal in length on the same plant. Flowering pedicels (1.3*–2.3–)3–5 mm long, slightly ascending or, more commonly perpendicular to the axis of the raceme, pubescent, with capitate and clavate-tipped, glandular hairs, 0.1–0.3 mm long, with or without a minute bracteole, to ca. 0.5 mm long, at the base. Fruiting pedicels 4–8(–12) mm long. Buds sparsely pubescent, rarely glabrous, with short, glandular hairs ca. 0.2 mm long; white, green or reddish-tinged, elliptic, oblong to obovate to narrowly obovate in outline, short

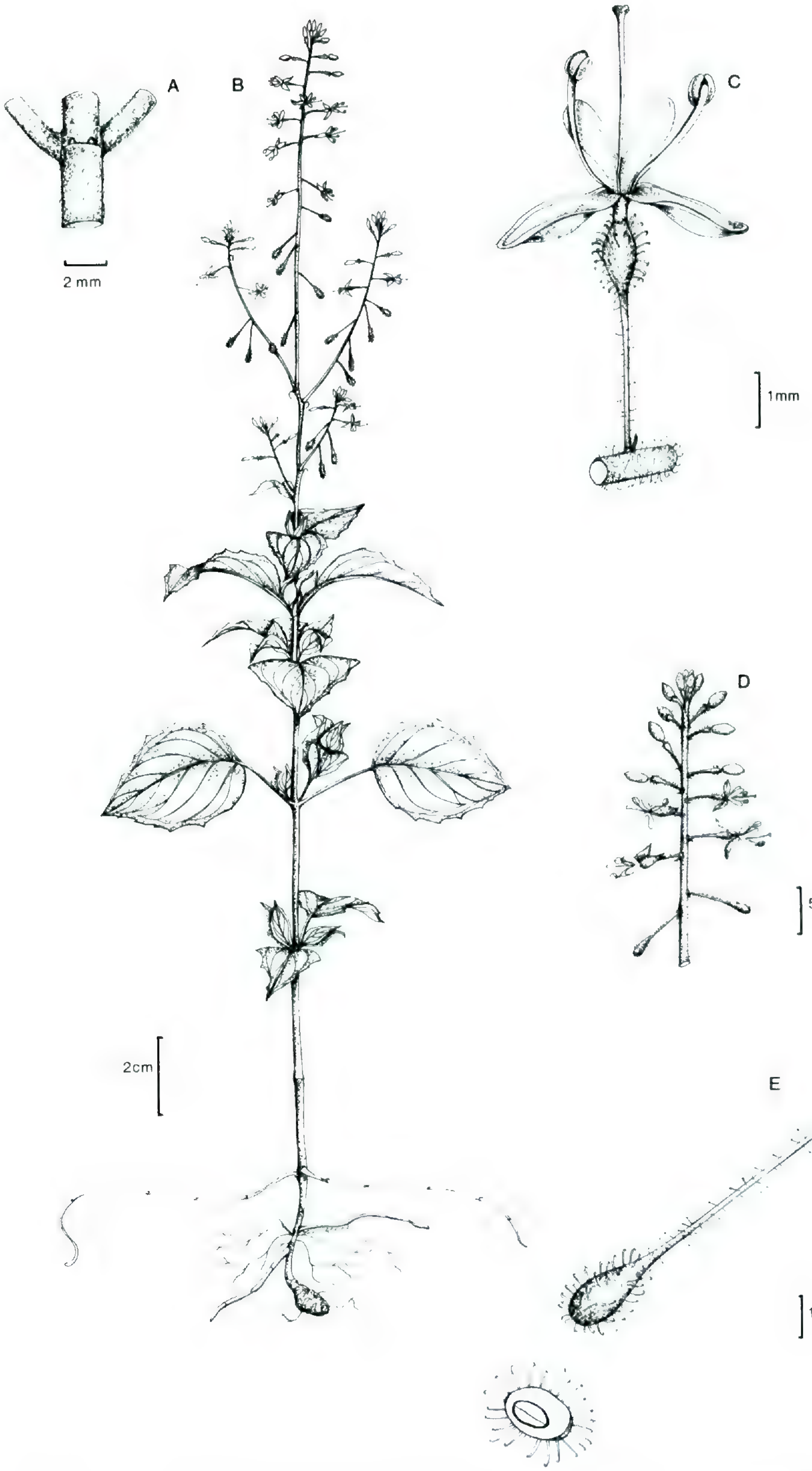


FIGURE 16. *Circaea repens* Wall. ex Asch. & Magnus.—A. Mid-stem node.—B. Habit.—C. Flower with petal removed; note absence of exserted nectary.—D. Inflorescence.—E. Fruit. From *Stainton 1380* (E).

acuminate to rounded at the apex, from the summit of the ovary, (1.9–)2.3–3.2 mm long, 0.7–1.5 mm thick just prior to anthesis. Ovary 1.3–1.5 mm long, 0.6–0.8 mm thick at anthesis, ellipsoid to obovoid, densely covered with soft, translucent, uncinate hairs. Floral tube (0.2*–)0.4–0.8 mm long, 0.2–0.3 mm thick at the narrowest point, funnelform. Sepals (1.1*–)1.8–2.5 mm long, (0.7*–)1.1–1.5 mm wide, pubescent on the abaxial surface, rarely glabrous, with hairs as on the buds; white, green or reddish-tinged; oblong to ovate, gradually rounded from above the middle to the obtuse or acute apex, spreading to reflexed in flower. Petals (1*–)1.4–2.3 mm long, (1*–)1.3–2(–2.9) mm wide, about as long as wide, white or pink, broadly to narrowly obtriangular in outline, V-shaped; the apical notch (0.5*–)0.7–1.4 mm deep, commonly ¾ the length of the petal. Stamens erect and parallel with the style or spreading at anthesis, subequal to or shorter than the style; filaments (1.8*–)1.9–3.4(–3.9) mm long; anthers 0.3–0.5 mm long, 0.3–0.4 mm thick. Style straight, erect, (2.2*–)2.6–4.2 mm long, topped by a shallowly bilobed, obtriangular stigma, ca. 0.4 mm tall, ca. 0.5 mm thick. Nectar secreting disc inconspicuous, wholly within the floral tube. Mature fruit (2.5*–)3.5–4.2 mm long, 0.9–1.6 mm thick, narrowly to broadly clavate, rounded at the apex, tapering smoothly to the pedicel, unilocular and 1-seeded, without prominent ribs and deep sulci, the surface smooth except for a shallow groove representing an extension of the pedicel on the dorsal surface; densely covered with stiff, translucent, uncinate hairs, 0.4–0.7 mm long, and with fewer, glandular hairs ca. 0.1 mm long. Fruiting pedicels spreading at right angles to the raceme axis to slightly reflexed. Combined length of pedicel and mature fruit, (6.8*–)7.5–15 mm long. Gametic chromosome number, $n = 11$. * Measurements of plants from Bhutan and Sikkim.

TYPE: Nepal, vicinity of Kathmandu, 1821, *N. Wallich 6341* (K, lectotype; BM, G, 2 sheets, K, W, isolectotypes).

Distribution (Fig. 17): Shade of moist to wet forests and brushy thickets or in moist open places. China, in western Hubei, south-central and southwestern Sichuan and Yunnan; Burma (1 collection); Bhutan, Nepal, and northeast India west nearly to Kashmir; Pakistan (one collection). Between (1,500) 2,300 and 3,300 m. Flowering early July to October and sporadically into early November.

Specimens examined:

BHUTAN. Punakha-Suchala, *S. Bowes Lyon 5049* (BM); Chukka Duupu, *R. E. Cooper 1256* (E); Chukka, *R. E. Cooper 1274* (BM, E); Dotena Limpu, *R. E. Cooper 3302* (BM, E); Nam Tamai valley (Adung Wang), *F. Kingdon-Ward 13510* (BM); Julu & Denchung Khoma Chu, *F. Ludlow et al. 21392* (BM, DS); near Ritang, *S. Nakao 835* (KYO).

CHINA. HUBEI: Shennongjia, *Shennongjia Exped. 10851, 31695* (PE). SICHUAN: environs of Ta-Tsien-lou, *M. Bonvalot & Prince Henri D'Orleans s.n.* (P); Emei Hsien, Emei Shan, *C. Y. Chiao & C. S. Fan 473* (A); Baoxing (P'ao-hsing) Hsien, *K. L. Chu 3242* (BM, E, NAS, W), *3381* (BM, E, PE, W), *3403* (PE), *3476* (BM, E, PE), *3481* (PE, W); Liang Shan, *Exped. Pl. Med. Sichuan 27961* (NAS); Emei Hsien, *Exped. Pl. Med. Sichuan 13228* (NAS); Hongxi Hsien, *C. T. Guan 6894* (PE); Emei Hsien, *Y. Y. Ho 5060* (NAS); Mt. Omei-shan, *E. Faber 71296* (US), *W. P. Fang 2805* (E); Shimian Hsien, *C. C. Hsieh 41977, 42033* (PE); Kangding Hsien, *C. P. Huang 1852* (PE); Honton R., *Potanin in 1885* (K, LE, P); Baoxing Hsien, *T. P. Soong 39263* (PE); Emei Hsien, *T. Tang & F. T. Wang 23310* (NAS), *T. H. Tu 476* (NAS, PE); Mt. Omei-shan, *F. T. Wang 23310* (GH), *E. H. Wilson 5767* (BM, P); Nanchuan Hsien, *J. H. Xiong 92550* (PE); Ebian Hsien, *C. W. Yao 2839* (NAS, PE); Leibo Hsien, *T. T. Yü 3685* (PE). XIZANG (Tibet): Meto Hsien, *Kokonor-Tibet Exped. 74-4902*

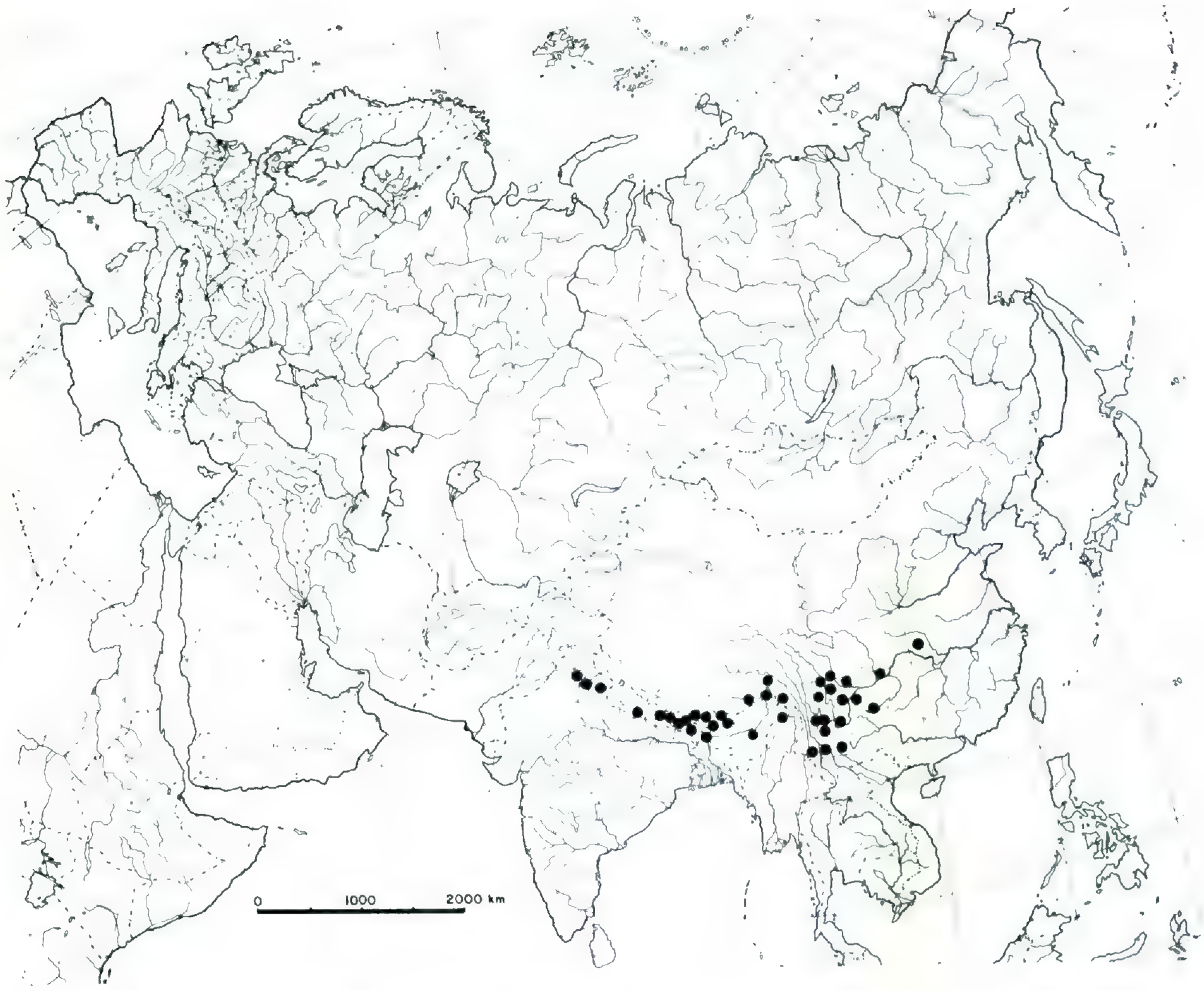


FIGURE 17. Distribution of *Circaea repens* Wall. ex Asch. & Magnus.

(PE); Milin Hsien, *Chin. Med. Exped. 3746* (PE); Nyalam Hsien, *Chin. Med. Exped. 1183, 1257* (PE); Nyingchi Hsien, *Chin. Med. Exped. 3594* (PE); Medog, *Qinghai-Xizang Exped. 744902* (PE); Zayu, *Qinghai-Xizang Exped. 73827* (PE); Milin Hsien, *Qinghai-Xizang Exped. 741941* (PE); Nyingchi, *P. C. Tsoong 3594* (PE); Tangmei Hsien, *T. S. Ying & D. Y. Hong 755* (PE); Cona Kian, *Xizang Exped. 751706* (PE). YUNNAN: San-tchang-kiou, Ho-kin, *P. Delavay 118* (P), *991* (A, MO, P, US); Pei-tsao-long-shan, *J. Delavay 6638* (K, MO, P); Liang-wang-shan, *J. Delavay 6903* (MO, P, US); Tong-tchouan, *F. Ducloux 244* (NY, UC), *1421* (E), *5395* (P), *6401* (P); E flank of the Lichiang Range, *G. Forrest 6261* (BM, E, S); Tong-tchouan, *E. E. Maire s.n.* (W), *in 1912* (G); Pe-long Tsin, *E. E. Maire in 1913* (G, P); Ten-choin-lin, *E. E. Maire 341* (E); Te-niou-kuen, *E. E. Maire 2991* (NY, UC); Chou-ke-suin, *E. E. Maire 3992* (UC); Talifu region, *C. Schneider 3098* (G, GH, K); Qiaojia Hsien, *B. S. Sun 948* (PE); "Yunnan," *T. T. Yü 7469* (A).

INDIA. ASSAM: Naga Hills, Japvo, *D. N. L. Bor 6444* (BM); above Ginjia, *J. R. Reid in 1885* (E). HIMACHAL PRADESH: Simla, *H. Collett in 1862?* (K), *C. B. D. s.n.* (E), *Dalhousie s.n.* (G); Simla, Cheop Forest, *G. Watt 7949* (E). SIKKIM: Lata, *H. Cave in 1912* (BM); Yumtang, *H. Cave 179* (K); Nubay, *C. B. Clarke 25324* (K); Lachen, *R. E. Cooper 395* (BM, E); Darjeeling, *J. M. Cowan s.n.* (E); Darjeeling, Gatribas, *H. Hara in 1964* (TI); Lachen, *J. D. Hooker in 1849* (K); 7–10,000 feet, *J. D. Hooker s.n.* (G, L, W); Gangri, *Dr. King's collector in 1887* (B); Chungtang, *Smith & Cave 2608* (B). UTTAR PRADESH: Nainital Cheena Peak, *P. Sehgal 57* (US); Kumaon, *R. Strachey & J. E. Winterbottom 1* (BM, GH, KP). STATE UNKNOWN: Jumna Valley, *J. F. Duthie 1048*(G); "Himal. Bor. Occ., 7–800 feet," *T. Thomson s.n.* (BM, G, GH, K, W); Tapa, *T. Thomson in 1849* (K); Tachoong, *T. Thomson in 1849* (G).

NEPAL. Chhange, *Banerji & P. R. Sakya 5750* (BM); Sheopuri, N of Kathmandu, *C. Chuma in 1970* (TI); Sinduwa, Dhankuta Dist., *H. Hara et al. in 1963* (TI); Batasay-Halhale, Bhangjang-Bhuspate Danra, *H. Hara et al. in 1963* (TI); Murhay, *H. Hara et al. 6300555* (TI); Sinduwa-Chitray, *H. Hara et al. 6300556* (KYO, TI); Rhikheswore, *S. B. Malla 229* (BM); Bagmati zone, before Syarpa-

gaon, N side of Langtang R., *D. Nicolson 2434* (US); Ganja La–Palchok Danda, *O. Polunin 1955* (BM); Golphubhanjang, *Shocollia & Sakya 3762* (BM); Mewa Khola, Tamur Valley, *J. D. A. Stainton 1308* (A, BM, E, UPS); Nr. Gurjakhani, *J. D. A. Stainton et al. 3658* (BM, G, P); Mardi Khola, *J. D. A. Stainton et al. 8420* (BM, E, UPS); Milke Bangyang, *L. H. J. Williams 1113* (BM); between Hururu & Num, Joljale Himal., Arun Valley, *T. Wraber 148* (BM); Yaba to Jiri, above Sikrigaon, *without collector in 1964* (A).

PAKISTAN. Chor, *R. C. s.n.* (LIV).

Circaea repens is recognized by the distinctive, deeply notched, V-shaped petals, unilocular ovaries and fruits, a nectary wholly within the floral tube, and by slender rhizomes with terminal, tuberous thickenings. *Circaea repens* resembles species with bilocular fruits in size and general appearance but is similar to the unilocular *C. alpina* in flower and fruit characters.

Ascherson and Magnus (1870) were the first to point out that the unilocular fruits could be used to separate *Circaea repens* from *C. lutetiana*. They failed to notice that the equally important character of presence or absence of an exserted nectar-secreting disc could also be used. Handel-Mazzetti (1933) was the first to point out that *C. repens* lacks a prominent disc, which is always present in *C. lutetiana*.

Wallich's collections, *6341* and *6342*, in his Numerical List (1832), differ only in that *6341*, which he called *Circaea repens*, is taller and with longer pedicels than his *6342*, which he thought to be Ehrhardt's *C. intermedia*. C. B. Clarke (1879), evidently without close examination of the flowers and fruits, assumed that the larger plants were identical to *C. lutetiana*, which they superficially resemble. Clarke did recognize that the smaller plants (*6342*) were different from *C. intermedia* but thought that they were closely allied to *C. alpina*, differing only in the pubescence of the stem. The specimen annotated by Clarke as *C. alpina* var. *himalaica* (K) differs somewhat from most specimens of *C. repens* in that its leaves are more crowded and cordate at the base, as is usual in *C. alpina* subsp. *alpina*.

Circaea repens appears to occupy an intermediate position in the genus, linking the bilocular and unilocular species. It resembles the former in stature, in holding the flowers perpendicular to the raceme axis at anthesis, and in appearing to be outcrossing. The unilocular fruits and ovaries and the formation of tubers at the tips of the rhizomes link it to the latter. It can also be seen in freehand sections that the fruit bears a trace of a second locule represented by a darkened line. The functional locule is located obliquely towards one side of the fruit. No trace of a second ovule is evident in freehand sections.

One collection from Bhutan, Dotena Limpu, *R. E. Cooper 3302* (BM, E), is unusual in that the inflorescence, pedicels, and buds are entirely glabrous. The characteristic petals and fruits, however, leave no doubt that the plants are *Circaea repens*. Some plants from Emei Shan, Sichuan, have the petals with a more shallow apical notch, shorter pedicels in flower and fruit, and shorter fruit plus pedicel length. Plants from China often have thicker and more prominently denticulate leaves. Plants from China and N Burma consistently lack bracteoles.

7. Circaea alpina L., Sp. Pl. 9. 1753.

Erect, or decumbent at the base and rooting at the nodes, 0.3–5 dm tall, simple or branched above or occasionally bushy-branched from near the base. Plants

forming numerous filiform rhizomes, each producing late in the season a tuberous thickening at the apex; the tubers giving rise to the following year's plants from their apices and to the following year's rhizomes from their nodes; filiform rhizomes occasionally arising from the lowermost nodes of the stem and then arching and ultimately becoming subterranean and tuber-forming, the aerial portions of the rhizomes occasionally with the scale-like leaves enlarged and similar to the stem leaves. Plants ranging from completely glabrous (populations of *C. alpina* subsp. *alpina*) to pubescent throughout (most populations of *C. alpina* subsp. *imaicola*). The stem with short, soft, falcately recurved hairs 0.1–0.2 mm long; the axis of the inflorescence with short capitate and clavate-tipped glandular hairs or with hairs as on the stem, or with an admixture of the two; the petioles with soft, short, upwardly curved, falcate hairs, these sometimes continuing along the veins above, and occasionally below, and also on the interveinal areas above, sometimes also with strigillose hairs admixed. Stems most commonly green, occasionally the nodes purple, rarely the entire stem purple (*C. alpina* subsp. *angustifolia* commonly has the axis of the inflorescence purple and the stem green). Leaves horizontally spreading, light green and translucent (in *C. alpina* subspp. *alpina, micrantha* and *pacifica*) or deep green and opaque (in *C. alpina* subspp. *angustifolia, caulescens,* and *imaicola*) or, in plants from the Himalayan region and China, with the area along the veins green and the interveinal areas red pigmented. Leaves near the summit of the stem the largest, (1–)1.5–6(–11) cm long, 0.7–5.5(–8) cm wide, abruptly reduced in size upward to the base of the inflorescence and ultimately bractlike and alternate, gradually to abruptly reduced downward, distantly to closely spaced and then appearing somewhat whorled. Leaf shape highly variable, from narrowly trullate or elliptic to nearly circular, acute to short acuminate at the apex, very narrowly cuneate to cordate at the base, subentire to very sharply serrate. Petioles 0.3–3(–4) cm long, terete or semiterete (in *C. alpina* subspp. *alpina, micrantha,* and *pacifica* the petiole is often flattened in pressing and appears winged), glabrous to densely pubescent with short, soft, upwardly curved, falcate hairs 0.1–0.2 mm long; with, or occasionally without, reduced branches arising in the axils. Inflorescence glabrous to densely pubescent with capitate and clavate-tipped glandular hairs 0.1–0.2 mm long or with soft, short, falcately recurved hairs 0.1–0.2 mm long, or with an admixture of the two; terminal on the main stem and simple or, more commonly, with one or more lateral branches from the base of the terminal raceme and at the tips of short axillary branches or arising directly from the axils of the uppermost leaves; the lateral branches alternate or opposite and subtended by reduced leaves or leaflike bracts. The terminal raceme, from the uppermost reduced leaf or leaflike bract, 0.7–2 cm long at initiation of flowering, to 12(–17) cm long at cessation of flowering; the lateral racemes 0.8–3 cm long at initiation of flowering, to 9(–15) cm long at cessation of flowering, subequal in length on the same plant. Flowering pedicel 0.7–3.5 mm long, perpendicular to the axis of the raceme (in *C. alpina* subsp. *caulescens* and some plants of subsp. *angustifolia*) to ascending or erect (in *C. alpina* subspp. *alpina, imaicola, micrantha, pacifica,* and some plants of *angustifolia*), glabrous or very rarely with a few, short, capitate and clavate-tipped glandular hairs ca. 0.1 mm long; with a minute setaceous bracteole, 0.1–0.4(–0.6) mm long at the base or (in *C. alpina* subsp. *caulescens* and some plants of subsp. *pacifica*), the bracteole lacking. Fruiting pedicels 1.5–5.2 mm

long. Buds glabrous, or very rarely glabrescent, with very short, soft, straight hairs ca. 0.1 mm long; white, pink, or purple-tinged apically or the entire bud pink or purple; elliptic to broadly so, ovate to broadly obovate in outline, smoothly rounded to the obtuse or minutely mammiform apex; from the summit of the ovary, 0.8–2.6 mm long, 0.4–1.3 mm thick just prior to anthesis. Ovary 0.5–1.5 mm long, 0.3–0.7 mm thick at anthesis, slenderly clavate to obovate in outline, glabrous (in *C. alpina* subsp. *micrantha*) or, more commonly, densely covered with short, soft, translucent, uncinate hairs. Floral tube from a mere constriction between the ovary and the base of the sepal lobes to 0.5(–0.6) mm long, 0.1–0.3 mm thick at the narrowest point, funnelform to very broadly so. Sepals 0.8–1.8 (–2.2) mm long, 0.6–1.3 mm wide, glabrous, white or pink, occasionally purple-tinged apically or rarely purple throughout; oblong, ovate to broadly so or triangular ovate, rounded to the obtuse or minutely mammiform apex; spreading perpendicularly to the ovary or slightly reflexed. Petals 0.6–2 mm long, 0.6–1.8 mm wide, from longer than broad to slightly broader than long; white, narrowly obtriangular, obdeltoid, obovate to broadly so to depressed obovate in outline; the apical notch essentially lacking to 0.7 mm deep, to ½ the length of the petal, the petal lobes rounded to truncate, or rarely the apices somewhat crenulate (in *C. alpina* subsp. *angustifolia*). Stamens erect, ascending or, less commonly, spreading at anthesis, as long as or slightly longer than the style; filaments 0.7–2.2 mm long; anthers 0.2–0.4 mm long, 0.2–0.4 mm thick, most commonly dehiscing before the buds open. Style straight, erect, 0.6–2.3 mm long, topped by an obtriangular to transversely oblong, bilobed stigma 0.1–0.4 mm tall, 0.15–0.5(–0.7) mm thick. Nectar-secreting disc wholly within the floral tube and inconspicuous. Mature fruit 1.6–2.6 mm long, 0.5–1.2 mm thick, clavate or obovate (in *C. alpina* subsp. *angustifolia*), rounded to subtruncate at the apex, tapering smoothly into the pedicel; unilocular and 1-seeded, without ribs or sulci but with the pedicel extending as a shallow groove along the upper surface; densely covered with soft to stiff uncinate hairs 0.2–0.5 mm long, these translucent or containing purple pigments (in *C. alpina* subsp. *angustifolia* and some plants of subsp. *micrantha*), and with fewer, short, clavate-tipped capitate hairs intermixed. Fruiting pedicels horizontally spreading perpendicular to the raceme axis to slightly deflexed at maturity. Combined length of pedicel and mature fruit, (3.5–)4–7.8 mm long. Gametic chromosome number, $n = 11$ (unknown in *C. alpina* subsp. *micrantha*).

Distribution: Moist places and on moss-covered rocks and logs, cold temperate and boreal forests at high latitudes and altitudes throughout the northern hemisphere to 70° N. Lat., extending into the subtropics and tropics at high elevations in southern Asia. From near sea level to 5,000 m. Flowering, mid-April to mid-September and sporadically to mid-October.

Circaea alpina can be distinguished from other species of the genus primarily by its unilocular, 1-seeded fruits, which lack any trace of a second locule. The species that most closely resembles *C. alpina* is *C. repens* of the Himalayan region, but the latter species is more robust and coarser, has a trace of a second locule in the fruits, has petals that are cleft more than half way to the base, and,

although the character is not as reliable, has leaves with 9–15 secondary veins while *C. alpina* has leaves with 5–10 secondary veins. Both *C. alpina* and *C. repens* bear tubers at the ends of the rhizomes and are the only species of the genus to do so.

In this treatment *Circaea alpina* is recognized as an inbreeding complex of six subspecies, each exhibiting different geographical or ecological preferences but with areas of overlap between two or more subspecies through parts of their range. These subspecies form a reticulate pattern of morphologically intergrading populations, some of which are separated only by seemingly minute differences. In other cases, were it not for numerous intermediate plants, some subspecies appear so dissimilar that it would be easily justifiable to recognize them as separate species, as has often been done in the past.

Although the characters that may be used to separate the subspecies are few, they are constant within geographical and/or ecologically distinct areas. The reticulate nature of variation between subspecies makes it difficult to determine phylogenetic relationships within *Circaea alpina* but it seems highly probable that subsp. *caulescens* is the most primitive since it retains a greater number of ancestral characters. Among these are the divergent or nearly divergent posture of the pedicels at anthesis, larger flowers, robust habit, thicker leaves, and pubescent stems, all characters found in species having bilocular and 2-seeded fruits and which are predominantly outcrossing. One puzzling feature, however, is the absence of a bracteole at the base of the pedicels in *C. alpina* subsp. *caulescens*, which is present in all other subspecies of *C. alpina* and in many of the species having bilocular fruits. It seems highly unlikely that *C. alpina* subsp. *caulescens* gave rise to the other subspecies of *C. alpina* but probable that plants ancestral to subsp. *caulescens* could have done so. The widely disjunct range of *C. alpina* subsp. *caulescens* at the present time seems to indicate that at some time in the past it had a much wider distribution; it is now restricted to a few favorable habitats in the Caucasus and Altai Mountains, central and Far Eastern Asia and in disjunct areas in Japan.

Loss of pubescence, a change of pedicel posture at anthesis from divergent to ascending or erect, reduction in leaf thickness, and a reduction in size of the flowers are derived conditions and are exhibited by *Circaea alpina* subsp. *alpina* and subsp. *micrantha*. The extreme narrowing of the leaves and the trend toward narrowly cuneate leaf bases in *C. alpina* subsp. *angustifolia* is also an advanced condition, but subsp. *angustifolia* remains primitive in bearing the flowers on divergent pedicels in many plants. *Circaea alpina* subsp. *angustifolia* intergrades with subsp. *imaicola* and it may possibly be that the divergent pedicels at anthesis in subsp. *angustifolia* are secondarily derived.

Circaea alpina is predominantly self-pollinating but with some degree of outcrossing as evidenced by the numerous hybrids between it and several of the species that bear bilocular fruits. In all cases where plants of *C. alpina* were observed in the field and in the greenhouse the anthers dehisce while still in the buds and while appressed to the stigma (see also Raven, 1963, and Haber, 1967, 1977). This adaptation apparently has helped *C. alpina* to occupy less favorable areas at high latitudes and altitudes where availability of insect visitors is often

lacking or reduced due to frequent periods of unfavorable weather. During long periods of cold, cloudy, or rainy weather effective pollination may occur, with the inflorescence elongating, the ovaries maturing, and the floral tube eventually dropping without the buds ever opening. This is certainly the case in *C. alpina* subsp. *alpina* in North America and in subsp. *imaicola*, which I observed during a period of very cold, rainy weather in the high mountains of Taiwan. The situation was different in plants of *C. alpina* subsp. *caulescens* in Japan on Hokkaido during a period of similar weather. In this subspecies all flowers opened despite the cold weather even though buds on plants of subsp. *alpina* that were growing nearby remained closed. *Circaea alpina* subsp. *caulescens* grows at relatively lower altitudes and/or latitudes than other subspecies and, as Skvortsov (1970a) has pointed out, and my own observations in Japan confirm, seems to prefer somewhat warmer habitats.

The critical temperature below which the buds of *Circaea alpina* subsp. *alpina* remain closed is between 14° and 16°C. This coincides closely with the lowest temperatures where activity ceases among the insects that frequently visit the flowers of *Circaea*. As temperatures rise, the buds tend to open progressively sooner after anther dehiscence and perhaps in some cases the buds may actually open shortly before anther dehiscence. The latter possibility would seem most likely in *C. alpina* subspp. *caulescens* and *angustifolia*, in which the flowers are held perpendicular to the raceme axis as in the outcrossing, less specialized species of the genus.

KEY TO THE SUBSPECIES OF *CIRCAEA ALPINA*

a. Inflorescence elongating as or before the flowers open; flowers more or less loosely spaced, the lower flower-bearing pedicels perpendicular to the raceme axis at anthesis ..... b
  b. Pedicels without a minute bracteole at the base, or the bracteole represented by a darkened gland; leaves ovate to broadly so, rounded to truncate or subcordate at the base; hairs on fruit translucent; Caucasus and Altai regions, Lake Baikal and central Far Eastern Asia ..... 7a. subsp. *caulescens*
  b. Pedicels with a minute bracteole, 0.2–0.5 mm long, at the base; leaves elliptic to trullate or ovate, narrowly to broadly cuneate at the base; hairs on fruit containing purple pigment; southwestern China ..... 7b. subsp. *angustifolia*

a. Inflorescence elongating after the flowers open; flowers clustered and corymbose at the summit of the raceme, the pedicels erect or ascending at anthesis c
  c. Stem pubescent, with at least a few, soft, falcately recurved hairs ..... d
    d. Leaves thick, deep green or reddish, opaque; Himalayan region, mountains of China and southern India; Taiwan ..... e
      e. Leaves elliptic to trullate, narrowly to broadly cuneate at the base ..... 7b. subsp. *angustifolia*
      e. Leaves ovate, rounded to subcordate at the base, rarely broadly cuneate ..... 7c. subsp. *imaicola*
    d. Leaves thin, pale green, translucent ..... f
      f. Ovaries minutely pubescent at anthesis; petals conspicuously notched; western North America ..... 7d. subsp. *pacifica*
      f. Ovaries glabrous at anthesis; petals emarginate or barely notched; Himalayan region and southwestern China ..... 7f. subsp. *micrantha*
  c. Stem glabrous ..... g
    g. Ovaries minutely pubescent at anthesis; petals conspicuously notched, the notch 0.3–0.7 mm deep, ¼–½ the length of the petal; wide ranging in the northern hemisphere ..... 7e. subsp. *alpina*
    g. Ovaries glabrous at anthesis; petals emarginate or barely notched, the notch to 0.3 mm deep, less than $^1/_5$ the length of the petal; very high elevations in the Himalayas and southwestern China ..... 7f. subsp. *micrantha*

7a. **Circaea alpina** L. subsp. **caulescens** (Komarov) Tatewake, Veg. Shikotan Is. 44. 1940.—FIG. 18.

Circaea alpina L. var. *imaicola* Asch. & Magnus, pro parte, Bot. Zeitung (Berlin). 28: 750. 1870.
Circaea alpina L. var. *caulescens* Komarov, Fl. Mansh. 3: 99. 1905.
Circaea imaicola (Asch. & Magnus) Hand.-Mazz., pro parte, Symb. Sin. 7: 603. 1933.
Circaea caulescens (Komarov) Nakai ex Hara, J. Jap. Bot. 10: 588. 1934.
Circaea caulescens (Komarov) Nakai ex Hara var. *robusta* Nakai ex Hara, J. Jap. Bot. 10: 589. 1934. TYPE: Korea, Province Kogen, Mt. Kongo-san, 7 August 1916, *T. Nakai* (TI, holotype).
Circaea caulescens (Komarov) Nakai ex Hara var. *pilosula* Hara. J. Jap. Bot. 10: 589. 1934. TYPE: Japan, Honshu, Prefecture Nagano (Prov. Shinano), Wada-toge Pass, 23 July 1880, *J. Matsumura* (TI, holotype).
Circaea alpina L. var. *pilosula* (Hara) Hara, J. Jap. Bot. 20: 326. 1944.
Circaea × *dubia* Hara var. *makinoi* Hara, J. Jap. Bot. 34: 317. 1959. TYPE: Japan, Honshu, Prefecture Tokyo (Prov. Musashi), Mt. Takao, 1921, *T. Makino* (MAK, holotype; S, TI, isotypes).
Circaea caucasica Skvortsov, Bull. Glavn. Bot. Sada, Moskva 77: 34. 1970. TYPE: U.S.S.R., Prov. Krasnodor (Olin Kuban), in Teberda R. valley, ca. 1,250 m, 2 July 1907, *E. A. Endaurova* (LE, holotype, not seen).

Plants 0.5–3.5 dm tall. Stem pubescent with short, soft, falcately recurved hairs 0.2–0.3 mm long, the petioles with similar but upwardly curved hairs, at least in lines along the upper surface, the leaves also with similar hairs along the main veins and frequently also on the interveinal areas on the upper surface. The stem, and less often the petiole, firm, terete, remaining unflattened in pressing, or occasionally the petioles flattened and appearing winged. Stem green or occasionally the nodes purple. Leaves deep green or bluish green, opaque; those between the middle and the summit of the stem the largest, 1.2–4.5 cm long, 0.6–3.5 cm wide; gradually to abruptly reduced upward to the base of the inflorescence and eventually bract-like, gradually to abruptly reduced downward, infrequently the leaves clustered near the summit of the stem and appearing whorled. Leaves ovate to broadly so to nearly deltoid, acute to short acuminate at the apex, rounded or truncate, less commonly subcordate or cordate at the base, shallowly to prominently dentate, the apex of the teeth commonly blunt; glabrous or, more frequently, pubescent along the main veins, and usually also on the interveinal areas above, with soft, short, falcate or strigillose hairs 0.1–0.2 mm long, also with slightly curved to falcate cilia along the margins. Petiole 0.5–3 cm long, subterete to terete, pubescent, at least in lines along the upper surface, with short, soft, upwardly curved falcate hairs 0.1–0.2 mm long; with or without reduced branches arising in the axils. Inflorescence glabrous or, rarely, with sparse, capitate and clavate-tipped glandular hairs ca. 0.1 mm long; terminal on the main stem and upper axillary branches, rarely at the tips of axillary branches arising from the base of the stem. The inflorescence simple or, more commonly, with alternate or opposite lateral racemes from the base, these subtended by reduced leaves or leaflike bracts. Flowering pedicels glabrous, 1–3.5 mm long, ascending or diverging perpendicular to the axis of the raceme; the flowers opening during or after the elongation of the raceme and ± widely spaced; with a minute setaceous bracteole, 0.1–0.2 mm long at the base or, more commonly, the bracteole absent and represented by a short, glandular process. Fruiting pedicels 2.5–3.8 (–5) mm long. Buds glabrous, ovate to very broadly elliptic to obovate in outline, obtuse or, less commonly, minutely mammiform at the apex; from the summit of the ovary, 1.3–2.2 mm long, 0.8–1.3 mm thick; white or pink, commonly purple

FIGURE 18. *Circaea alpina* L. subsp. *caulescens* (Komarov) Tatewake.—A. Habit.—B. Inflorescence.—C. Flower.—D. Fruit.—E. Mid-stem node. From *Boufford & Wood 19782* (CM, KYO, MHA, MO, PE, UC).—F. Habit of plant from the Caucasus. From *Skvortsov in 1976* (MO).

tinged at the apex. Ovary 0.7–1.1 mm long, 0.3–0.6 mm thick at anthesis, clavate to narrowly so; pubescent, with soft, short, translucent, uncinate hairs. Floral tube 0.2–0.4 mm long, 0.1–0.2 mm thick at the narrowest point, funnelform to very broadly so. Sepals (1–)1.4–1.9 mm long, (0.6–)0.8–1.3 mm wide, white or pink, commonly tinged with purple at the apex; narrowly to broadly ovate or oblong ovate, rounded to the obtuse or, rarely, minutely mammiform apex. Petals (0.9–)1.4–2 mm long, (0.9–)1.2–1.9 mm wide, from longer than wide to wider than long, white or pink, obovate to depressed obovate or obdeltoid in outline, the apical notch 0.4–0.7 mm deep, ⅓–½ the length of the petal; the petal lobes rounded. Filaments 1.8–2.2 mm long; anthers 0.2–0.4 mm long, 0.3–0.4 mm thick. Style 1.8–2.5 mm long; stigma 0.2–0.4 mm tall, 0.2–0.5 mm thick. Mature fruit clavate, 1.8–2.6 mm long, 0.7–1.1 mm thick, the translucent uncinate hairs 0.3–0.4 mm long. Combined length of pedicel and mature fruit, 5–6.2(–7.9) mm long. Gametic chromosome number, $n = 11$.

TYPE: China, in the valley of the Yalu River, 10 July 1897, *V. Komarov* (LE, lectotype).

Distribution (Fig. 19): Moist places, on moss-covered rocks and logs or in drier soils in cool temperate deciduous and mixed forests and the lower part of boreal forests. Japan (Hokkaido, mountains of central Honshu and Mt. Kurotaki-yama, Shikoku); Korea, northeastern and east-central China and southeastern U.S.S.R.; disjunct on the south side of Lake Baikal and in the Altai and Caucasus Mountains. From near sea level to 1,500 meters. Flowers, from mid-June to mid-August and sporadically to mid-September.

Representative specimens examined:

U.S.S.R.

RUSSIAN S.F.S.R. Coast of Tatary, *Bushnell in 1856* (BM); Novina-Ompo, *N. Dessoulavy 4940* (G); from Amur to Tirma R., Lake Tyrmy, *W. Docturowsky 1279* (UC); Sajan, Urika R. near Angari R., W Hudgera, *Krivotulenko 580* (ALTA); Primorski Prov., Spassk-Dolny Dist., *V. Dvorakovskaya & L. Vavilova in 1973* (MHA); Amur, Oettu, *C. Maximowicz in 1859* (L); Khabarovsk Prov., near Khekhtsurskiya, *A. Nechayev 38* (MHA); Khabarovsk Prov., Sovetskaya Dist., Gavan, near Tubutchi Station, *A. Nechayev 158* (MHA); Lake Klepochnoi (Suifuna), *M. N. Nefelova & R. A. Pashchenko in 1952* (MO); Primorski Prov., Terney Dist., Sichote-Alin Reservation, *Shemetova 1190a* (MHA); Primorski Prov., vicinity of Vladivostok, *A. K. Skvortsov in 1967* (MO); N Caucasus Mts., Kabardino-Balkaria, near Chegem, *A. K. Skvortsov in 1976* (MO); Altai, NW extremity of Teletskoye Lake, *A. K. Skvortsov in 1977* (MO); Primorski Prov., Cape Gamov, *G. Smirnova 2211* (DS); Vladivostok & vicinity, *D. Topping 2292* (US); Vladivostok Dist., Vladivostok, *Voinovich & Kriger in 1910–1914* (MHA); Primorski Prov., Terney Dist., near Amgu, *V. N. Voroshilov in 1969* (MHA); Primorski Prov., Svetlaya, *V. N. Voroshilov 507* (MHA); Khabarovsk Prov., Lazo Dist., SE of Khabarovsk, Bitcheraya, *V. N. Voroshilov 12501* (MHA); Primorski Prov., Chasan (Khasan) Dist., Cape Gamova, *V. N. Voroshilov 6530* (MHA); "Coast of Manchuria, lat. 44–45° N," *C. Wilford in 1859* (GH, K, S, US); Primorski Prov., Sutschan Dist., near Ustschanovka, *without collector in 1969* (MO).

ASIA

CHINA. ANHUI: Mt. Huang-shan, *C. Chien 1221* (W), *R. C. Ching 4230* (UC), *T. N. N. Liou & P. C. Tsoong 3151* (PE), *H. Wissmann in 1936* (W). HEBEI: East Tomb, *H. F. Chow 40677, 40733* (PE); Beijing ("Peking"), *A. David in 1863* (BM); Zhaulu Hsien, *W. Y. Hsia 2353* (PE), Tung-ling, East Tomb, *C. F. Li 11215* (NAS, NY, PE); Xiaowutai Shan, *T. C. Li 2668* (PE); Laiyuan Hsien, *K. M. Liou 2903* (NAS, PE), *3180* (PE); Fuping Hsien, *K. M. Liou 3058, 3586* (PE); Wuling Shan, *T. N. Liou 6955* (NY); East Tomb, *T. N. Liou 6956* (PE); Neiqui Hsien, *H. Y. Liu 555* (NAS); Chih-li, Po-hua Shan, *J. C. Liu 1132* (UC); Neiqui Hsien, Xiaowutai Shan, *Y. Liu 13146* (NAS, PE); Mt.

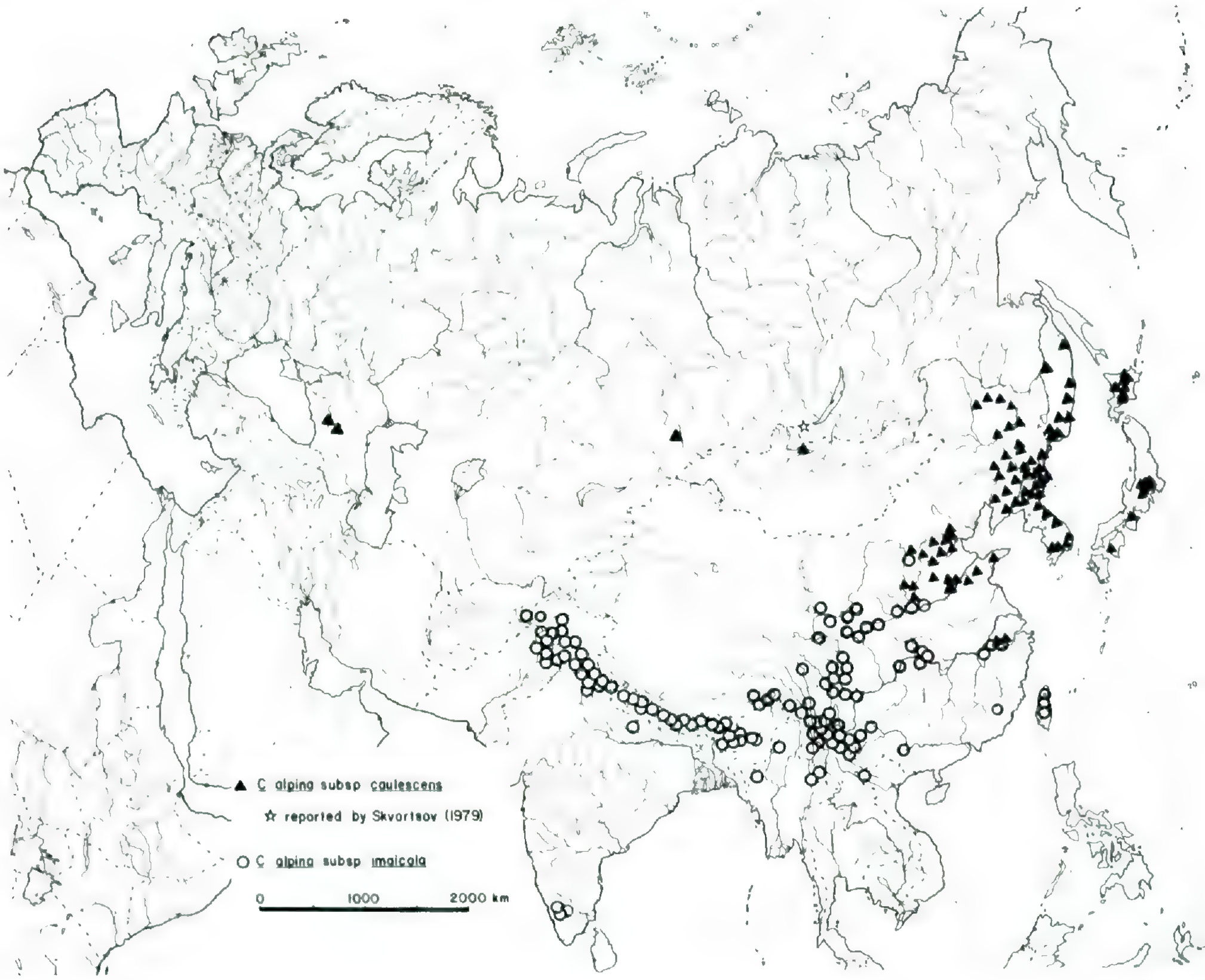


FIGURE 19. Distribution of *Circaea alpina* L. subsp. *caulescens* (Komarov) Tatewake (solid triangles; report by Skvortsov (1979), solid circle), and *C. alpina* L. subsp. *imaicola* (Asch. & Mag.) Kitamura (open circles).

Murei, Sansei-sho, *I. Miyake s.n.* (TI); Ch'eng-te, Mt. Murei, *T. Nakai et al. in 1933* (TI); Chih-li, Pai-t'a, *H. Serre 2598* (W); Xiaowutai Shan, Yang-kia-p'ing, Yung-lin, *H. Smith 639* (LD, S, UPS); Nekka Prov., Mt. Murei-san, *M. Takahashi in 1933* (TNS); East Tomb, *H. T. Tsai 50304* (PE); Pao-feng-tze, Baihua Shan, *C. W. Wang 60172* (PE), *60840* (A, PE), *61689, 61802* (PE); Xiaowutai Shan, *C. W. Wang 61820* (PE); Wuling Shan, *W. C. Wu & C. Y. Yang 59* (PE); Xiaowutai Shan, *W. C. Wu 2681* (PE); Bohua Mt., *Y. Yabe in 1905* (NAS); Baxing Hsien, *C. Y. Yang 1015* (PE). HEILONGJIANG: I-ch'un Hsien, Wu-ying, *T. T. Chung & C. O. Liu 7864* (PE); Xiao Hinggan Ling, *W. Z. Fang 479* (NAS); at R. Mai-ho super, *N. Kozlow 14434* (W); near Shitokheza Station, *D. Litvinov 2066* (NY); Koandei-san, Siao Hingua Ling, San-ko-sho, Tangwang-ho, *S. Nakao in 1943* (KYO); Yichun Hsien, *Sino-German Exped. 7864* (PE); Dailing, *C. S. Sung* 192 (PE); near village of Laochunlatun; *K. C. Wang 603* (LE); Harbin city, *B. C. Wu in 1959* (NAS); Tung-pei Tui, *without collector* (PE-315740). JILIN: from Mukden to Kirin, Chang-pei-shan and to Tang-ho-ko, *H. E. M. James in 1886* (K); Omoso Dist., U-cre-sun-che valley, *V. Komarov in 1896* (BM); Ninguta Dist., Czau-lin Mts., *circa* Taimagou, *V. Komarov in 1896* (K); Omoso Dist., Eze-sun-che valleys, *V. Komarov 1138* (TI); Lao-ye-ling, *E. Licent 8505* (BM); Changbai Mt., *T. N. Liou 1719* (NAS); Dailing, *C. S. Sung s.n.* (PE); Changbai Shan, *J. J. Xian 420, 476* (PE). LIAONING: Fusong Hsien, *Y. L. Chang 141, 230, 314* (PE), *T. N. Liou 1353* (PE); "Port Bruce," *C. Maximowicz in 1860* (K, NY); Hentauhetze, *B. V. Skvortsov in 1937* (GH); "Liaoning," *Z. Y. Wu 1353* (NAS). SHANDONG: 500 km S of Beijing ("Pekin"), *L. Chanet & J. H. Serre 2598* (P); Fei Hsien, Mt., Meng Shan, *T. Cheo & L. Yen 343* (GH); T'ai-an-fu, Mt. Tai Shan, *M. S. Clemens 1450* (E); "San-ton Prov.," *U. Nagai 56* (TI); Tai Shan, *S. C. Tsui 75* (PE); Lao Mt., *Y. Yabe in 1919* (NAS); summit of Mt. Tai Shan, *Y. Yabe in 1925* (TI). SHANXI: Yuanqu Hsien, *S. Y. Bao 2239* (PE); Hsiuyuan Hsien, *K. C. Kuan et al. 839* (PE); Wutai Shan, *K. C. Kuan & Y. L. Chen 1687, 2487* (PE); Hoang-ts'ao-keou, *E. Licent 604* (BM, K, P, W); Tsiliyü at Mt. Ho

Shan, *E. Licent 12071* (ND, W); Hsiatschuan, Mt. Yao Shan, *E. Licent 12733* (GH, W); Yüan-ch'ü Dist., Shui-wang-p'ing, *H. Smith 6700* (UPS); Fou-p'ing, Mei-hei-t'ouo Mt., *without collector A192* (S). "MANCHURIA": Badao-heza valley, *V. Komarov in 1896* (LE); at the Lu-t'a R., *V. Komarov in 1935* (W); Khatokheza, *D. Litvinov 2741* (UC); at the Amur R., *R. Maack 486* (GH); "Manchuria," *C. Maximowicz & Schrank s.n.* (NY).

JAPAN. HOKKAIDO: Iburi, Tomakomai Experimental Forest of Hokkaido Univ., *D. E. Boufford & E. W. Wood 19658* (CM, E, G, KYO, MHA, MO, PE, SHIN), *19662* (BM, CAS, CM, E, K, KYO, MHA, MO); Kushiro, Kawakami-gun, Shibecha-cho, Shibecha Experimental Forest of Kyoto Univ., *D. E. Boufford & E. W. Wood 19761* (KYO, MO); Abashiri, Abashiri-gun, Tsubetsu-cho, NW side of Lake Chimikeppu-ko, *D. E. Boufford & E. W. Wood 19782* (CM, KYO, MHA, MO, PE, UC), *Class of 1953* (SAP), *M. Hirano in 1952* (KYO); Hidaka, along Chiroio R., *Y. Hoshino in 1933* (SAP); Iburi, Tomakomai Experimental Forest of Hokkaido Univ., *M. Hotta 16814* (KYO); Abashiri-gun, Tsubetsu-cho, Kamisato, *T. Matsuki in 1970* (MAK); Abashiri-gun, Tsubetsu-cho, Lake Chimikeppu-ko, *T. Matsuki in 1971* (MAK); Ishikari, Soumbetsu, *K. Miyabe & M. Tatewaki in 1925* (SAP); Kitami, Tokoro-gun, Rubeshibe-cho, *G. Murata & Y. Momotani 439* (KYO); Ishikari, Sounkyo, *T. Nakai in 1928* (TI); Nopporo, *T. Tanaka 243* (GH); Hakkan, *M. Tatewaki in 1921* (SAP); Kushiro, Lake Kutcharo, Motoko-san, *M. Tatewaki 20038* (SAP); Tokachi, Ashiyose, Kamiwashi-bu to Berabonai-to, *M. Tatewaki in 1951* (SAP); Ishikari, Biei to Matsuyama, *K. Togashi in 1918* (SAP); Kitami, *K. Uno 15696* (GH); Ogawa, *Yokoyama in 1937* (SAP). HONSHU. NAGANO PREFECTURE: Matsumoto city, Sanjiro pasture to Mt. Chausu-yama, *D. E. Boufford et al. 19624* (CM, KYO, MHA, MO, S); Matsumoto city, Tobira-onsen, *D. E. Boufford et al. 19627* (CM, DS, E, KYO, MHA, MO, NCU); Suwa-gun, Shimo-suwa-cho, Wada-toge, *D. E. Boufford et al. 19628* (KYO, MHA, MO); Togakushi, *U. Faurie 1336* (KYO, P); Sugadaira, *H. Hida in 1939* (TI); Minamisaku-gun, Kawakami-mura, from Senjogahara to Jumonji-toge, *M. Hotta 10231* (KYO); Mt. Togakushi, *Iisiba in 1908* (TAI); Tobira Pass, Utsukushi-gahara-kogen, Matsumoto city, *S. Ito 636* (TNS); Suwa city, Kirigamine to Yashima, *S. Kobayashi 1344* (MAK); Wada-toge, *J. Matsumura in 1880* (TI); Mt. Togakushi, Hyakken, *M. Minemura 588* (MAK); Mt. Hachibuse, *S. Momose in 1929, in 1930* (TI); Utsukushi-gahara, *S. Momose in 1929* (TI); Shimoina-gun, Ooshika-mura, Sawai, *M. Muramatsu 1722* (TNS); Mt. Togakushi, *G. Murata 6411* (KYO, SAP), *T. Nakajima in 1913* (TUS), *H. Nishida in 1977* (MHA, MO); Minamisaku-gun, Aiki, Mt. Ogura, *K. Ohwi* 67 (TI), *K. Sato 800* (TI); Shinshu-toge, *D. Shimizu in 1939* (TNS); Mt. Utsukushi-gahara, Kurumi-zawa valley, *S. Suzuki 362* (A); Shimoina-gun, Toyama-gawa, Fukagasawa, *T. Yamazaki in 1954* (TI); Karosawa, near Mt. Yatsuga-dake, *without collector in 1925* (MAK 117737); Onata-gun, Mada-mura, Utsukushi-gahara, *without collector in 1929* (MAK 117704); Mt. Togakushi-san, *without collector in August* (KAG). NARA PREFECTURE: Yoshino-gun, Mt. Ohmine, Mt. Daifu-dake, *H. Koyama & M. Hotta 5471* (KYO, MO); Yoshino-gun, Ohmine Mts., *T. Shimizu 4408* (SHIN). SHIZUOKA PREFECTURE: Suruga, Minami-Alps, Dentsuku-toge, *J. Sugimoto in 1953* (TNS); Surugu, Mt. Fuji-san, *without collector* (TNS 13226). TOCHIGI PREFECTURE: Nikko, *J. Bisset 4225* (BM, E), *H. Muramatsu in 1923* (TI). TOKYO PREFECTURE: Minamitama-gun, Mt. Yakao, *T. Makino in 1921* (MAK, S, TI). YAMANASHI PREFECTURE: Daibosatsu Pass, *C. Kosaka 14* (TI); Minami-kuma-gun, Tentsuki Pass, *Matsuda & Fujita in 1954* (TI); Mt. Azusa-yama, Azusashiraiwa, *D. Shimizu in 1939* (TNS). SHIKOKU. KOCHI PREFECTURE: Takaoka-gun, Niyodo-mura, Mt. Kurotaki-yama to Mt. Tengunomor, *G. Murata 17303* (KYO, SHIN, US).

KOREA, NORTH. Kogen Prov., Mt. Kariou-san, *S. Hozawa in 1941* (TNS); Kankyo-hokudo, Mt. Hakuto-zan, *T. Ishidoya in 1931* (KYO); Kogen-do, Kongo-san, *G. Koidzumi in 1932* (KYO); Kakyo-do, Nanyo village, *G. Koidzumi in 1933* (KYO); N Kakyo-do, foot of Mt. Tosei-san, *G. Koidzumi in 1933* (KYO); Heian-hokudo, Mt. Myoko, *G. Koidzumi in 1935* (KYO); Yellow R., San-su Dist., Onkol-niuri valley, *V. Komarov in 1897* (P); upper Yellow R., Czan-dshin-gan, *V. Komarov in 1897* (NY); Utsuryo Island, Nanyo-do, *T. Nakai 4460* (TI); Mt. Kongo near Matsukiri, *T. Nakai 5686* (TI); Mt. Kambo, *T. Nakai 7281* (TI); Kankyo-nando, Nishi-osuiri, *N. Nomura in 1935* (KYO); Saikarei, *Y. Oguma in 1914* (TNS); Kankyohokudo, Takado, *J. Ohwi 2708* (TNS); Kongo-san, *S. Okuyama in 1940* (TNS); Kankyonando, Choshin-gun, Toukamen Tounho, Ankirikoku, *A. Yamamoto in 1934* (TNS).

KOREA, SOUTH. Kan'an, Mt. Senbutsu, *M. Honda 39* (TI); Chollanan-do, Kwangju, *U. Hurusawa in 1943* (TI); Pyonganpuk-do, Unsan, *T. Ishidoya 11* (TI); See Chun Dong, *R. G. Mills in 1910* (UC); Cho-san, *R. G. Mills 387* (TI); Kyongsangnan-do, Mt. Chii, *T. Nakai in 1913* (TI); Kokai, Shoto, *T. Nakai 13302* (TI); Keishonan-do, Mt. Chii, *S. Okamoto 17928* (KYO), *17929* (KYO, TNS), *17932* (KYO, TNS); S Chulla Prov., Mt. Chii, *Mrs. R. K. Smith in 1928* (US), *in 1934* (GH), *76* (GH, TI), *77* (TI), 685 (US); Keishonan-do, Chii-san, *K. Uno 23366* (GH); Kangwon-do, Sepo, *without collector 10711* (MICH).

KOREA. Localities unknown: Kangwongpuk-do, Kumgang, *M. Kobayashi 41* (TI); Mt. Surl-ack, *I. K. Lee in 1957* (MO); Hamkyongnan-do, S foot of Chapek Bong, *T. Nakai 15601* (TI); Ryangkang-

do, Daehungli-sanyo, *T. Nakai 3639* (TI); Hamkyongpuk-do, Kyongsung, Tuulonpoli, *T. Nakai 7282* (TI); Kangwongpuk-do, Kumgang, *T. Nakai 17179* (TI); Kangwongpuk-do, Mt. Gumgang-san, *T. Uchiyama in 1902* (TI); Shayurei, *O. Yoichiro in 1914* (TNS).

MONGOLIA. Ta-tchiao-chan, *A. David 2334* (P); Selenge Dist., 25 km SW of Selenge, *N. Dorofeyur 343* (LE).

Circaea alpina subsp. *caulescens* is distinguished by the pubescent stems, a usually glabrous inflorescence, dark-green or bluish-green leaves that are usually pubescent above and flowers that open after elongation of the raceme axis and are held on pedicels that diverge perpendicular to the axis of the raceme. Bracteoles are most commonly lacking. In its extreme forms it approaches *C. alpina* subsp. *alpina* in one direction and subspp. *imaicola* and *pacifica* in another. *Circaea alpina* subsp. *alpina* differs from subsp. *caulescens* in having the stems completely glabrous and in having bracteoles at the base of the pedicels. In a few cases bracteoles are present at the base of a few pedicels in subsp. *caulescens* but are rarely present beneath every pedicel of a raceme. *Circaea alpina* subsp. *pacifica* differs in having thinner, pale green, translucent leaves, a glandular pubescent raceme axis, and in the position of the flowers at anthesis. In *C. alpina* subsp. *pacifica*, the flowers open before elongation of the raceme and are held in a corymbose cluster at the summit of the raceme on erect or ascending pedicels. *Circaea alpina* subsp. *imaicola* differs by having bracteoles always present at the base of the pedicels, a usually pubescent raceme axis, and in the smaller flowers held in an erect ascending position as in *C. alpina* subspp. *alpina*, *pacifica*, and *micrantha*.

The very few specimens I have seen of plants from the Caucasus Mts., which Skvortsov (1970, 1977) called *C. caucasica* (Fig. 18) are, except for being slightly larger in a few floral features, indistinguishable from *C. alpina* subsp. *caulescens*. The slightly larger fruits and sparse glands in the inflorescence and slightly longer pedicels are only minor differences that one would expect in such a widely disjunct and separately evolving population. The Siberian collection, *Dorofeyur 343*, 25 km S of Selenge (LE), is similar to the collections of Skvortsov from the Caucasus region that Skvortsov called *C. caucasica*.

Plants of *Circaea alpina* subsp. *caulescens* from Japan are generally smaller in stature than plants from the Asian mainland but usually larger than adjacent plants of subsp. *alpina* when they are found growing together. In Japan, *C. alpina* subsp. *caulescens* prefers drier and more exposed habitats than subsp. *alpina* and in central Honshu subsp. *caulescens* grows at lower elevations, usually below 1,400 meters. Skvortsov (1970) found the situation to be similar in the eastern U.S.S.R., but gave no mention of altitudinal differences. It seems likely that *C. alpina* subsp. *caulescens* had a more continuous range in Japan during the Pleistocene. With warming conditions following the last glaciation *C. alpina* subsp. *caulescens* migrated northward, where it is now fairly widespread on Hokkaido, and upward into favorable mountainous areas farther south on Shikoku and Honshu, while becoming extinct in the intervening lowland areas. Its absence from many seemingly suitable areas in other mountainous regions of Honshu is unexplainable.

7b. Circaea alpina L. subsp. **angustifolia** (Hand.-Mazz.) Boufford, stat. nov. Based on *C. imaicola* (Asch. & Magnus) Hand.-Mazz. var. *angustifolia* Hand.-Mazz., Symb. Sin. 7: 603. 1933.—FIG. 20.

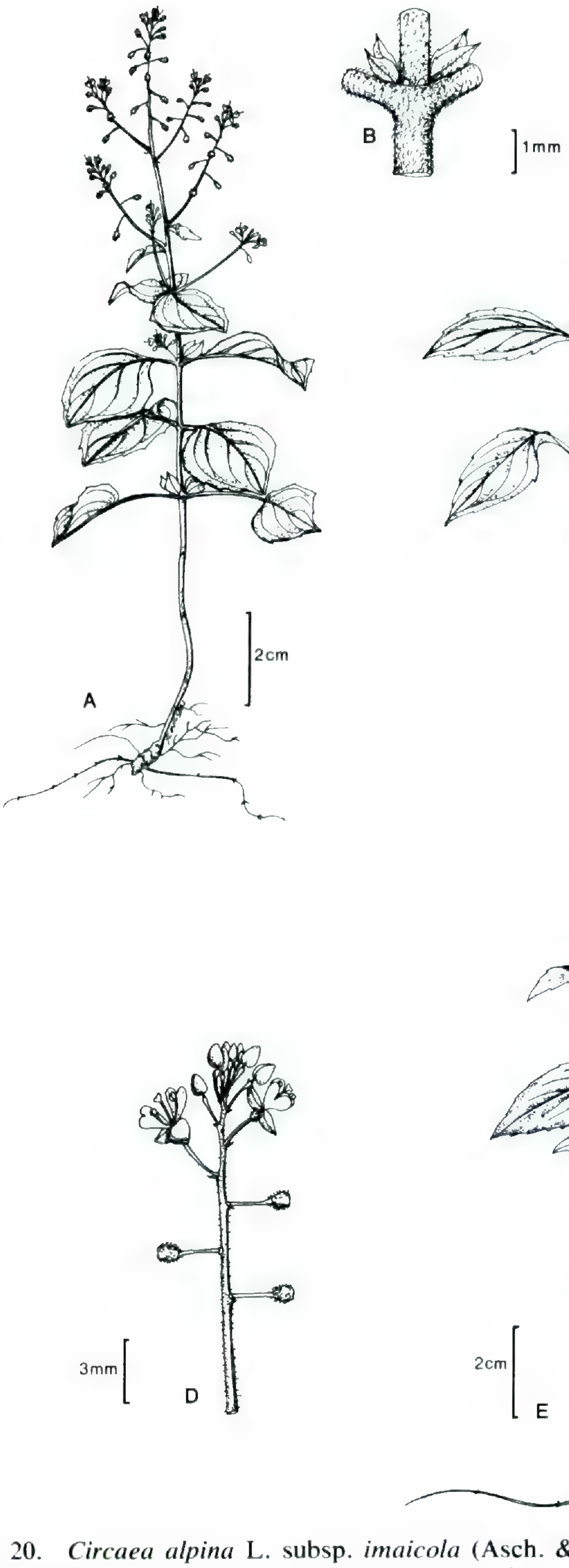


FIGURE 20. *Circaea alpina* L. subsp. *imaicola* (Asch. & Magnus) Kitamura.—A. Habit.—B. Node of stem. From *Polunin et al. 382* (UPS). *Circaea alpina* L. subsp. *angustifolia* (Hand.-Mazz.) Boufford.—C. Stem. After *Maire 6363* (LE).—D. Inflorescence.—E. Habit. From *Maire 295* (BM, E).

Circaea lutetiana L. race *erubescens* (Franchet & Savat.) H. Lév. var. *mairei* H. Lév., Bull. Acad. Int. Géogr. Bot. 22: 219. 1912. TYPE: China, Yunnan, mountain forests, August 1905, *E. E. Maire 397* (UC, lectotype).

Circaea imaicola (Asch. & Magnus) Hand.-Mazz. var. *mairei* (H. Lév.) Hand.-Mazz., Symb. Sin. 7: 603. 1933.
Circaea pricei Hayata var. *mairei* (H. Lév.) Hand.-Mazz., Symb. Sin. 7: 1376. 1936.

Plants 0.7–3.5 dm tall. Stem pubescent with short, soft, falcately recurved hairs 0.1–0.2 mm long; the petioles with similar but upwardly curved hairs; the leaves also with similar hairs and sometimes with short strigillose hairs in addition; the axis of the inflorescence most commonly glabrous or with short capitate and clavate-tipped glandular hairs. Stem green or occasionally purple, firm, terete, remaining unflattened in pressing. Leaves deep green or sometimes reddened, when reddened the areas near the veins remaining lighter in color, opaque; those between the middle and summit of the stem the largest, 1.4–4.5 cm long, 0.6–2.2(–3) cm wide, becoming gradually to abruptly reduced upward to the base of the inflorescence and ultimately bractlike and alternate, gradually reduced downward, never closely spaced and appearing whorled. Leaves elliptic or trullate to broadly trullate or ovate, very rarely broadly ovate, acute at the apex, narrowly to broadly cuneate at the base, shallowly denticulate, the teeth obtusely tipped; glabrous or, more commonly, pubescent on the veins above and usually also on the interveinal areas with soft, short, falcate hairs, 0.1–0.2 mm long, and sometimes also with strigillose hairs, 0.1–0.3 mm long, intermixed, the undersurface glabrous or, less commonly, with soft, short falcate hairs along the veins; the marginal cilia nearly straight to falcate, 0.1–0.3 mm long. Petioles 0.3–1.8 cm long, terete, only slightly flattened in pressing and never appearing winged; pubescent, with short, upwardly curved, falcate hairs, 0.1–0.2 mm long; with or without reduced axillary branches arising in the axils. Inflorescence glabrous or pubescent, with short, soft, capitate and clavate-tipped glandular hairs, 0.1–0.2 mm long; terminal on the main stem and uppermost axillary branches; purple or occasionally green. The inflorescence simple or with opposite or, more commonly, alternate lateral racemes from the base, these subtended by reduced leaves or leaflike bracts. Flowering pedicels 1.3–3.5 mm long, glabrous or, very rarely, sparsely pubescent with short glandular hairs ca. 0.1 mm long; ascending or diverging perpendicular to the axis of the raceme, the flowers opening during or after elongation of the raceme and ± widely spaced; with a setaceous bracteole, 0.3–0.5 mm long, at the base. Fruiting pedicels 2.4–5.2 mm long. Buds glabrous, from the summit of the ovary, (1.2–)1.5–1.9 mm long, 0.9–1.2 mm thick, white or pink, often purple tinged at the apex, very broadly elliptic, ovate to broadly obovate in outline, rounded at the apex. Ovary 0.6–1.3 mm long, 0.3–0.7 mm thick, clavate to obovate in outline, pubescent, with soft short, uncinate hairs containing purple pigment, rarely glabrous at anthesis. Floral tube 0.2–0.3 mm long, 0.2 mm thick at the narrowest point, broadly to very broadly funnelform. Sepals (0.8–)1.2–2 mm long, (0.6–)0.8–1.3 mm wide; white or pink, purple tinged at the apex, less commonly purple throughout, broadly to very broadly ovate or oblong ovate, rounded to the obtuse apex. Petals (0.7–) 1.1–2 mm long, (0.6–)1–1.7 mm wide, longer than wide, white or pink, narrowly to broadly obovate in outline; the apical notch 0.2–0.4 mm deep, $^1/_5$–$^1/_3$ the length of the petal; the petal lobes rounded, truncate, or minutely crenulate. Filaments 0.9–1.8 mm long; anthers 0.2–0.3 mm long, 0.2–0.3 mm thick. Style 1.3–2.3 mm long; stigma 0.2–0.4 mm tall, 0.3–0.5(–0.7) mm thick. Mature fruit obovoid to clavate, rounded to

truncate at the apex, 1.6–2.5 mm long, 0.8–1 mm thick; the uncinate hairs 0.2–0.3(–0.5) mm long, translucent but containing purple pigment. Combined length of pedicel and mature fruit, 4.5–6(–7.4) mm long. Gametic chromosome number, $n = 11$.

TYPE: China, Yunnan, Tung-ch'uan ("Tong-tchouan"), 2,700 m. September 1913, *E. E. Maire 1005* (E, holotype; BM, isotype).

Distribution (Fig. 21): Moist, open hillsides, thickets and forests in the mountains of southwestern China (Yunnan). Between 2,000 and 3,000 m. Flowers, July to mid-September and sporadically to mid-October.

Specimens examined:

CHINA. YUNNAN: Ta-li, Mt. Che-tcho-tze, Ta-pin-tze, *J. M. Delavay 1* (MO, P); Che-shan, Ki-chan, near Ta-pin-tze, *J. M. Delavay 4018* (A); Ta-ping ("Ta-pin-tze"), *J. M. Delavay 4776* (MO, P); Ch'eng-chiang ("Tchong-chan"), *F. Ducloux 239* (UC); Lan-ngy–tsin near Lou-lan, *F. Ducloux 240* (UC), *F. Ducloux 6015* (P); Hsiang-yun ("Yunnan-sen"), *F. Ducloux 604* (P); La-i-chang near Lou-lan ("Lan-ngy-tsin"), *F. Ducloux 1060* (E); Tou-ta, *F. Ducloux 2806* (NY); Tchong-chan, *F. Ducloux 3631* (P); Ho-ch'ing and Li-chiang valleys, *G. Forrest 562* (E); Ming-kuang valley, *G. Forrest 8637* (E, K); mountains of the Chung-tien Plateau, *G. Forrest 10860* (E, K); between Dsaodjiing and Hwadung, Dsolin-ho R., *F. Handel-Mazzetti 4969* (E, US, W); Pai-han-lo ("Bahan, pe-ha-lo"), at Salwin R., *F. Handel-Mazzetti 9577* (E, W); Mt. Tung-chuan, *E. E. Maire 295* (BM, E), *E. E. Maire 613* (BM, E), *E. E. Maire 1005* (BM, E), *E. E. Maire 2875* (NY, UC), *E. E. Maire 6363* (LE), *E. E. Maire in 1912* (G), *E. E. Maire in 1913* (G, P); humid forests on the plains, *E. E. Maire 1213* (P); on old moist moss, *E. E. Maire 2365* (E, K); K'un-ming ("Yunnan-fu"), *O. Schoch 306* (G, K); Lou-choci-tang, Yunpe, *S. Ten 87* (E, UC); Kubi, *S. Ten 1277* (W); Beyendjing, forests of Kubi, *S. Ten 1314* (W); Wei-hsi Hsien, *C. W. Wang 67687* (A); Mekong-Salwin divide, Bahanlo, *T. T. Yü 22709* (A, E).

Circaea alpina subsp. *angustifolia* may be recognized by its slender leaves with narrowly to broadly cuneate bases, the usually purple raceme axis, purple pigment within the uncinate hairs of the fruit, and in the flowers opening with or after elongation of the raceme so that the flowers are held on ascending or perpendicularly spreading pedicels. *Circaea alpina* subsp. *angustifolia* occurs completely within the range of subsp. *imaicola*, overlaps the range of subsp. *micrantha* in several places, and intergrades in different ways with each of these subspecies.

Circaea alpina subsp. *micrantha* only occasionally has the uncinate hairs of the fruits containing purple pigments but often has the raceme axis purple. Glabrous ovaries at anthesis occur commonly in subsp. *micrantha* but rarely in subsp. *angustifolia* (one example being *Maire 613*, E). *Circaea alpina* subsp. *micrantha*, however, differs in having narrowly to broadly ovate or triangular leaves with sharp, prominent serrations along the margins and with cordate bases, smaller floral parts, the petals emarginate or notched less than one fifth the length of the petal, and the raceme axes densely glandular-pubescent. The flowers are held in more or less tight clusters at the apex of the raceme on ascending or erect pedicels and open before elongation of the raceme. Plants of *C. alpina* subsp. *micrantha* usually occur at higher elevations (3,100–5,000 m) than do plants of subsp. *angustifolia*.

Plants of *Circaea alpina* subsp. *imaicola* differ in having ovate to orbicular-ovate leaves with truncate to broadly cuneate bases and the flowers clustered at

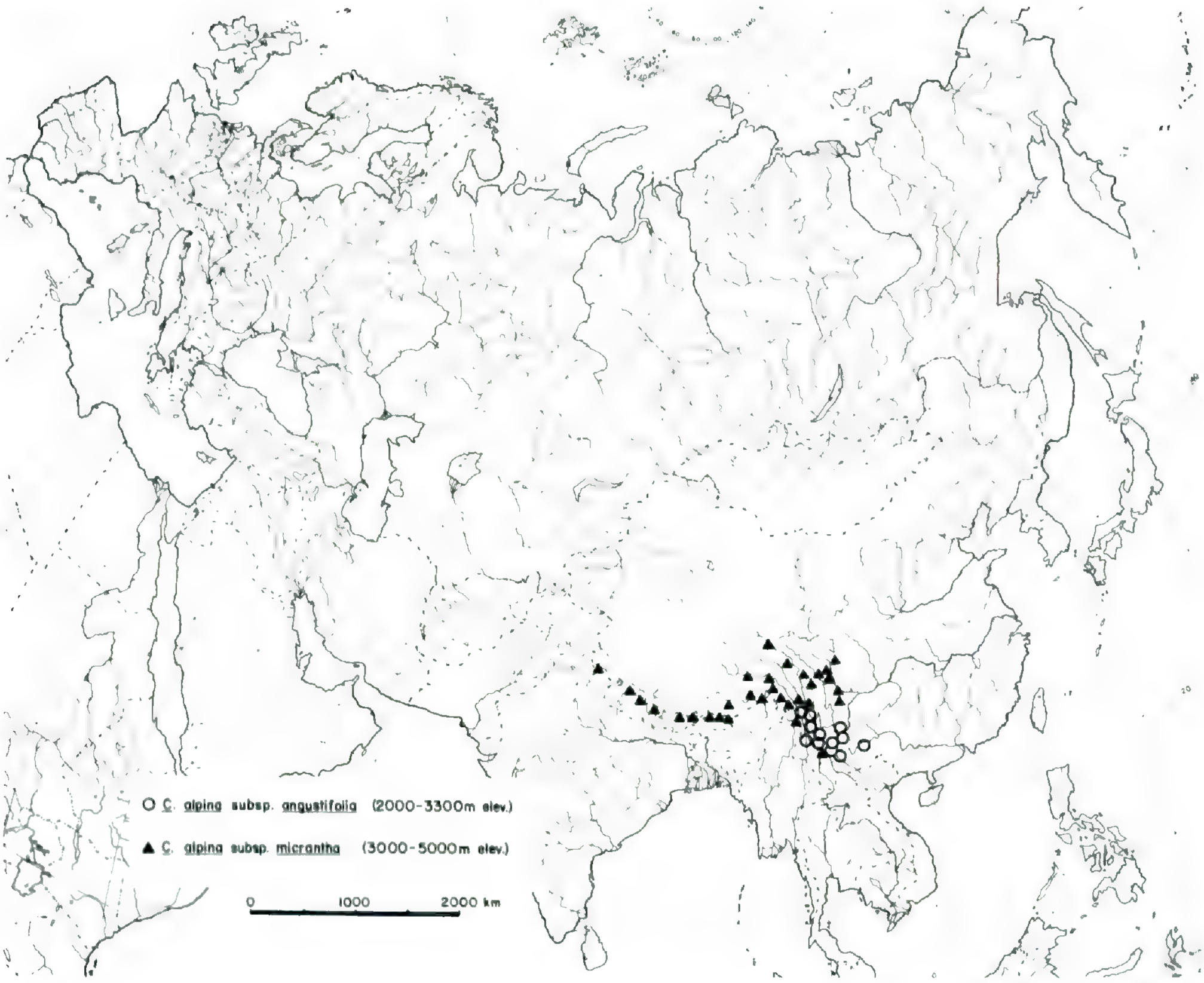


FIGURE 21. Distribution of *Circaea alpina* L. subsp. *angustifolia* (Hand.-Mazz.) Boufford (open circles) and *C. alpina* L. subsp. *micrantha* (Skvortsov) Boufford (closed triangles).

the apex of the raceme and opening before elongation of the raceme axis. The uncinate hairs of the fruits never contain purple pigment.

Circaea alpina subsp. *angustifolia* resembles subsp. *caulescens* in manner of opening and size of the flowers but differs in leaf shape and in having bracteoles always present at the base of the pedicels.

Plants that Handel-Mazzetti called *Circaea imaicola* var. *angustifolia* and *C. imaicola* var. *mairei* represent two extremes of variation within *C. alpina* subsp. *angustifolia*. At one extreme are plants with very narrowly cuneate leaf bases, lanceolate leaves, pubescent stems, glandular inflorescences, and with the uncinate hairs of the fruits without purple pigment. These grade into plants with broadly cuneate leaf bases, ovate leaves, glabrous inflorescences, and with the uncinate hairs of the fruits containing purple pigment. In the former, some plants have the flowers borne on ascending pedicels at anthesis, whereas in the latter the flowers are always borne on spreading pedicels. Examples of plants that are intermediate between the two extremes are the following: *Ducloux 2636* (P), *Ducloux 1060* (E), *Ducloux 240* (UC), *Maire 2365* (E, K, UC), *Maire in October 1913* (P), *Maire 295/1914* (BM).

Circaea alpina subsp. *angustifolia* is apparently endemic in Yunnan, China,

and is puzzling in that it shows no clear connection to any of the other subspecies of *C. alpina*, even though it combines the characteristics of several. In the position of the flowers it resembles *C. alpina* subsp. *caulescens* and is primitive in that respect and in having retained the minute bracteole at the base of the pedicels. Vegetatively it is advanced in having very narrow leaves with cuneate bases and in having purple pigment in the uncinate hairs of the fruit. It seems most likely that *C. alpina* subsp. *angustifolia* arose early in the evolution of the *Circaea alpina* complex and has evolved independently of the other subspecies. Another possibility is that the position of the flowers at anthesis is a secondarily derived condition and that subsp. *angustifolia* could have evolved from ancestral plants similar to *C. alpina* subsp. *imaicola*.

7c. Circaea alpina L. subsp. **imaicola** (Asch. & Magnus) Kitamura, Fl. Afghanistan 279. 1960.—FIG. 20.

Circaea alpina L. var. *imaicola* Asch. & Magnus, Bot. Zeitung (Berlin). 28: 749. 1870.
Circaea pricei Hayata, Ic. Pl. Formosa 5: 72. 1915. TYPE: China, Taiwan, A-li-shan ("Taltaka, Horisha"), 1,800 m, 9 July 1912, *W. R. Price 810* (TI, lectotype; K, 2 sheets, probable isolectotypes).
Circaea imaicola (Asch. & Magnus) Hand.-Mazz., Symb. Sin. 7: 603. 1933.
Circaea minutula Ohwi, Acta Phytotax. & Geobot. 2: 151. 1933. TYPE: China, Taiwan, Tai-chung Hsien, Hattsukan, 9 July 1933, *J. Ohwi 3868* (KYO, holotype; TI, isotype).
Circaea taiwaniana S. S. Ying, Alpine Pl. Taiwan in Color 2: 199. 1978. This is most likely *C. alpina* L. subsp. *imaicola* (Asch. & Magnus) Kitamura. TYPE: China, Taiwan, Maboulaseshan, alt. 3,100 m, *S. S. Ying 2751* (deposition of type not given and type not seen).

Plants (0.35–)0.7–3(–4.5) dm tall. Stem densely to sparsely pubescent with short, soft, falcately recurved hairs 0.1–0.2 mm long, rarely subglabrous; the petiole with similar but upwardly curved hairs; the leaves, at least along the veins above, also with similar hairs and also sometimes with longer strigillose hairs to 0.4 mm long; the inflorescence densely to sparsely pubescent with short, soft, capitate and clavate-tipped, glandular hairs or with hairs as on the stem, or an admixture of the two. The stem, and less so the petiole, firm, terete, remaining unflattened in pressing, or occasionally the petioles flattened and appearing slightly winged. Stem green or occasionally the nodes purple. Leaves deep green or bluish green, opaque; those between the middle and the summit of the stem the largest, 2–5(–7) cm long, 1.4–3.2(–4.5) cm wide; becoming gradually to abruptly reduced upward to the base of the inflorescence and ultimately bractlike, gradually to abruptly reduced downward; the leaves very rarely clustered near the summit of the stem and appearing whorled. Leaves ovate to broadly ovate, less commonly orbicular ovate, acute to very short acuminate at the apex, broadly cuneate to subcordate, but most commonly truncate or rounded at the base, subentire to occasionally prominently dentate, the apex of the teeth usually blunt; pubescent, rarely glabrous, with short, soft, falcate hairs 0.1–0.2 mm long, at least on the veins above, and sometimes also beneath, occasionally also with longer, 0.2–0.4 mm long, strigillose hairs intermixed, also with straight to falcate cilia along the margins. Petiole 0.7–3(–3.5) cm long, terete or subterete, pubescent, rarely glabrous, with soft, short, upwardly curved, falcate hairs 0.1–0.2 mm long; with or without reduced branches arising in the axils. Inflorescence pubescent, less commonly glabrous, with short, soft, capitate or clavate-tipped, glandular hairs 0.1–0.2 mm long or with hairs as on the stem or with an admixture of

the two, terminal on the main stem and upper axillary branches, very rarely at the tips of axillary branches arising from the base of the stem. The inflorescence simple or, most commonly, with alternate or occasionally opposite lateral racemes from the base, these subtended by reduced leaves or leaflike bracts. Flowering pedicels glabrous, 0.6–2.5 mm long, erect or ascending; the flowers opening before elongation of the raceme and clustered at the apex; with a minute setaceous bracteole, 0.2–0.4 mm long, at the base. Fruiting pedicels 2.5–4(–5) mm long. Buds glabrous or rarely glabrescent, oblong to oblong-obovate to very broadly obovate in outline, obtuse or, less commonly, minutely mammiform at the apex; from the summit of the ovary 1–1.2 mm long, 0.6–0.8(–1) mm thick, white or pink or sometimes pink tinged only at the apex. Ovary 0.9–1.3 mm long, 0.3–0.6 mm thick, clavate; pubescent, with soft, short, translucent, uncinate hairs or occasionally glabrous. Floral tube from a mere constriction to 0.3 mm long, 0.2 mm thick at the narrowest point, funnelform to broadly so. Sepals (0.7–)0.9–1.6 mm long, 0.8–1.1 mm wide, white or pink or pink tinged only at the apex, oblong to ovate, rounded to the obtuse apex. Petals 0.5–1.8 mm long, 0.7–1.5 mm wide, longer than wide, white or pink, narrowly to broadly obovate in outline, the apical notch 0.2–0.5(–0.7) mm deep, ¼–½ the length of the petal; the petal lobes rounded. Filaments (0.4–)0.8–1.6 mm long; anthers ca. 0.2 mm long, ca. 0.2 mm thick. Style (0.5–)0.8–1.8 mm long, stigma 0.2–0.3 mm tall, 0.2–0.5 mm thick. Mature fruit clavate, 2.1–2.5 mm long, 0.5–1.1 mm thick, the translucent uncinate hairs 0.3–0.5 mm long. Combined length of pedicel and mature fruit 4–6(–7) mm long. Gametic chromosome number, $n = 11$.

TYPE: India, eastern peninsula, *Wight 989* (K, lectotype; G, GH, GOET, L, LE, not seen, S, W, isolectotypes).

Distribution (Fig. 19): Cool, moist places along streams, in thickets, in deciduous and coniferous forests in mountainous areas. Central and southwestern China, northwestern Vietnam, northeastern and northwestern Burma and Assam, India, westward along the south face of the Himalayas to northeastern Afghanistan; disjunct in Taiwan and in the mountains of southern India. From 1,500 to 2,300 m in southern India, 2,000 to 4,000 m elsewhere. Flowers, July to mid-September, sporadically to mid-October.

Specimens examined:

AFGHANISTAN. Nuristan, Chatrass, *S. Kitamura in 1955* (KYO).

BANGLADESH. "E Bengal," *Griffith 2231* (GH, L, S, W).

BHUTAN. *F. Ludlow & Sherrff s.n.* (BM); near Bumthang, *F. Ludlow et al. 16978* (BM, E, G, UPS); Bumthang, *F. Ludlow et al. 19529* (BM, E, UPS); Rudd La, W side, *F. Ludlow et al. 20969* (E, UPS).

BURMA. Naung Chaung valley, *F. Kingdon-Ward in 1914* (E); Mindat, *F. Kingdon-Ward 22628* (BM); S Shan State, Kuy Tung, *R. W. MacGregor 796* (E).

CHINA. ANHUI: Mt. Huangshan, *R. C. Ching 8617* (ND, US), *8623* (ND, US), *61857* (NAS), *K. C. Kuan 75279* (PE), *P. C. Tsoong 3714* (PE). FUJIAN: Wuyi Shan, *C. P. Tsien 400618* (PE). GANSU: Yuzhong Hsien, *Hwanghe Exped. 3228, 3505* (PE); Lapuleng, *K. T. Fu 1227, 1648* (PE); Tetung, *Przewalsky 694* (P); Lapuleng, *T. P. Wang 5792* (PE); Min Hsien, *T. P. Wang 4646* (PE); Jiangyuan Hsien, Lung-te-kou, *T. P. Wang 17050* (PE). HENAN: Lushi Hsien, Lao-chun-shan, *K. M. Liou 5130, 5217* (PE); Song Hsien, *H. M. Shih 34939* (PE). HUBEI: Shennongjia, *Z. S. Chang & K. S. Fu 1008* (NAS, PE); S Badong ("Patung"), *A. Henry 6086* (GH, K, NY); Fang, also Hsing-shan, *A. Henry*

6906 (BM, K, NY); Shennongjia, *Shennongjia Exped. 21964, 31749, 32361* (PE). JIANGXI: Lu Shan, *M. J. Wang 826* (NAS). QINGHAI: Datong Hsien, *K. M. Liou 5959* (PE); Tongren Hsien, *T. P. Wang 6177* (PE). SHANXI: Ningwu Hsien, *Shanxi Exped. 1618* (PE). SHAANXI: Huanglong Shan, *K. T. Fu 3355* (PE); Taipaishan, *P. C. Tsoong 2511* (PE). SICHUAN: Baoxing Hsien, *X. S. Chang 7210* (PE); Jinchuan Hsien, *X. S. Chang 7210* (PE); Miyi, *S. Y. Chen et al. 10903, 11056, 11181* (NAS); Tien-chuan, K'ang-ting, Hsi-k'ang, *H. L. Chiang 265937* (PE); Tsio-ha-ping, Konting trip, *C. Y. Chiao 2072* (A); Ebian, *T. S. Choa s.n.* (NAS); Eshan, *T. Y. Chou & K. C. Hsu 472* (NAS); Emei Shan, *T. Y. Chou & K. C. Hsu 482* (NAS); Baoxing Hsien, *K. L. Chü 3242, 3381, 3476* (PE); Fuxiong Hsien, *Econ. Pl. Exped. 4501, 4510* (PE); Dawi Hsien, *Exped, Pl. Med. Sichuan 15376, 15728* (NAS); Zolge, *Exped. Pl. Med. Sichuan 20383* (NAS); Tchen-keou-tin, *R. P. Farges s.n.* (P); N of Yungning, Muli Monastery, *F. Handel-Mazzetti 7358* (US, W); "Szechwan," *A. Henry 8950* (K); Mao Hsien, *C. Ho & T. L. Chow 14003* (NAS); Li Hsien, *C. Ho & T. L. Chow 13284, 14003* (PE); Emei Shan, *Y. Y. Ho 6286* (NAS); Tainig Hsien, *W. G. Hu 10925* (PE); Dawu Hsien, *W. G. Hu & C. Ho 10964, 11026* (PE); Tianquan Hsien, *X. L. Jiang 35594, 38023* (PE); Heishui Hsien, *X. L. Jiang 73397, 77080* (PE); Dajin Hsien, *X. L. Jiang 78236* (PE); Aba Hsien, *H. Li 74080* (NAS); Heishui Hsien, *H. Li 74080* (NAS, PE); Daijin, *H. Li 78705* (NAS); Jinfo Shan, *K. F. Li 63026* (PE); Kangding Hsien, *C. S. Liu 1140* (PE); Kangding ("Tachienlu"), *A. E. Pratt 436* (BM, K, P), *590* (BM, K), *650* (P); Drogochi, *H. Smith 4715* (UPS); K'ang-ting, Cheto-la, *H. Smith 10948* (S, UPS); "Tibet oriental," *J. A. Soulie in 1895* (K, NY); Tung-o-lo, Kiala, *J. A. Soulie 364* (G); Kangding ("Ta-Tsien-lou"), *J. A. Soulie 364* (P), *2347* (P); Mt. Emei Shan, Chi-tien-chiao, *S. C. Sun & K. Chang 1085* (A); Nanping Shi, *Y. C. Tang et al. 104* (PE); Dege, *Y. W. Tsui 5111a, 5126* (PE); Chi-na-tung, Tsa-wa-rung, *C. W. Wang in 1935* (TAI), *65191, 65232* (A); Emei Shan, *F. T. Wang 23310* (PE), *23395* (GH, LE, PE); "W Szechwan," *E. H. Wilson 4462, 5167* (A); Barkam, *C. L. Wu 32728* (PE); Li Hsien, *C. L. Wu 33498* (PE); Shimian Hsien, *C. S. Xie 41972* (PE); Jinchuan Hsien, *J. M. Xue 15* (PE); Weixi Hsien, *K. H. Yang 58887* (PE). TAIWAN: Hualien Hsien, Mt. Hohuan Shan, *D. E. Boufford et al. 19320* (CM, K, KYO, MHA, MO, NCU); Hualien Hsien, Ta-yu-ling, *C. Chuang & M. Kao 4430* (NY); Chiayi Hsien, Ta-ta-chi to Pai-yunn Hostel, *C. C. Hsu 6259* (TAI, TI); Taichung Hsien, Chika to 369, *T. C. Huang & C. F. Hsieh 7164* (TAI); Chiayi Hsien, Mt. Yu-shan, *R. Kanehira & S. Sasaki in 1927* (TAI); Nantou Hsien, between Ten-tsu & Yin-hai, *M. T. Kao 5861* (TAI), *T. C. Huang et al. 5859* (TAI); Chiayi Hsien, Mt. Yu-shan ("Mt. Morrison"), *T. Kawakami 2030* (TAI); Taipei Hsien? ("Prov. Taipei"), upper Tai-ko-ke R., *K. Kojima & T. Shioma 2033* (KYO); Chiayi Hsien, Mt. Yu-shan, from Haiunsanso to Ton-pu, *H. Koyama 23957* (E, SHIN, TNS); Nantou Hsien, Neng-kao-shan ("Noko-zan"), *E. Matuda 255* (TI); Nantou Hsien, Yu-shan, *A. Ohno 1701* (KANA); Ilan Hsien, Mt. Nan-hu-ta-shan ("Nankotai-san"), *J. Ohwi 3938* (KYO); Tainan Hsien, Ali-shan ("Taltaka"), *W. R. Price 810* (K); Ilan Hsien, Mt. Nan-hu-ta-shan, *S. Sasaki in 1923* (TAI); Ilan Hsien, Lo-tung, *S. Sasaki in 1928* (TAIF); Hsinchu Hsien, Mt. Ta-pa-chien-shan, *T. Shimizu 20264* (SHIN); Hualien Hsien, *T. Suzuki 15041* (PE); Tainan Hsien, between Numanohira & Ali-shan ("Tataka"), *M. Tagawa 320* (KYO, TNS); Ilan Hsien, Mt. Nan-hu-ta-shan, between Kamibajin & Kirettoi, *M. Tamura et al. 20880* (SHIN); Ilan Hsien, Mt. Nan-hu-ta-shan, between Kirettoi & Kamibajin, *M. Tamura et al. 20988* (KYO, SHIN, TI); Nantou Hsien, from Tung-pu to Patungkuan, *M. Tamura et al. 22016* (SHIN); Nantou Hsien, Mt. Yu-shan, from Patungkuan to summit, *M. Tamura et al. 22085* (SHIN); Chiayi Hsien, en route from Tataka to Ali-shan, *M. Tamura et al. 22223* (SHIN); Nantou Hsien, Mt. Neng-kao-shan, between Tien-chih & Yun-hai, *M. Tamura & H. Koyama 23406* (KYO, S, TNS); Ilan Hsien, Nan-hu-ta-shan, Kietei-Bunakkei, *T. Yamazaki et al. 316* (TAI, TI); Ilan Hsien, Nan-hu-ta-shan, *T. Yamazaki et al. 385* (TI); Chiayi Hsien, Ali-shan, Paiyunshan-chuang, *T. Yamazaki & F. Yamazaki 790* (TI); Hualien Hsien, Mt. Hohuan-shan, *S. Ying 1289, 4882* (NTUF); Chiayi Hsien, Mt. Yu-shan, *S. Ying 1461* (NTUF); Ilan Hsien, Mt. Nan-hu-ta-shan, *S. Ying 2081* (NTUF); Hsinchu Hsien, Ta-pa-chien-shan, *S. Ying 4217, 4219, 4221, 4225* (NTUF). XIZANG (Tibet): Bomi Hsien, *Y. T. Chang & K. Y. Lang 449* (PE); Zhamo, *Y. T. Chang & K. Y. Lang 610* (PE); Nyingchi Hsien, *Y. T. Chang & K. Y. Lang 1333* (PE); Milin Hsien, *Kokonor-Tibet Exped. 74-1941* (PE); Gyala, *F. Ludlow et al. 5353* (BM, E, UPS); Kongbo Prov., Kulu Phu Chu, *F. Ludlow et al. 5947* (BM, E); Kongbo Prov., Nyoto Sama, *F. Ludlow et al. 15583* (BM, E, UPS); Zayu, *Qinghai-Xizang Exped. 731016* (PE); Medog, *Qinghai-Xizang Exped. 743977* (PE); Mainling Hsien, *Qinghai-Xizang Exped. 3908, 4097, 741941, 750876, 750878* (PE); Bienpa Hsien, *D. D. Tao 11203* (PE); Najia Hsien, *P. C. Tsoong 6718* (PE); Tsawarung, *C. W. Wang 65191, 65232* (PE); Yigong Hsien, *J. S. Ying & T. Y. Hong 542* (PE); Bomi Hsien, *J. S. Ying & T. Y. Hong 925* (PE). YUNNAN: Kunming ("Yunnan-fu"), *J. Cavalerie in 1919* (S, UPS); Likiang, *A. L. Chang & S. W. Yu 100982* (KUN); Fumin Hsien, *B. Y. Chiu 596142* (PE); Kunming, *B. Y. Chiu 771291* (KUN); Chungtien, *Chungtien Exped. 847, 1027, 1297* (PE); Mao-kon-tchang, *J. Delavay 54* (MO, P); Chiao-ch'e-tong, Hei-shan, *J. Delavay in 1885* (P); Hoking, Kona-lu-po, *J. Delavay 117, 119* (P); Ma-eul-shan, *J. Delavay 3856* (P); Yo-lin-shan, *J. Delavay 6533* (MO, P); Tse-tsa-long, *J. Delavay 6630* (US); Liang-shan ("Leang-ouang-shan"), *J. Delavay 6907* (P); Lung-i ("Lang-ngy tsin"), *F. Ducloux 2636* (P, US); Wuding Hsien, *Exped. Pl. Trop. Yunnan 60-141* (NAS); SE Chung-tien, between Anangu & Bodo, *K. M. Feng 2048* (A); Li-

chiang Range, E flank, *G. Forrest 2922* (E); Tali Range, E flank, *G. Forrest 4748* (BM, E, P); Li-chiang Range, E flank, *G. Forrest 6332* (BM, E), W flank, *G. Forrest 6338* (BM, E, P); Mekong-Salween divide, *G. Forrest 19644* (E, UC, US, W); Li-chiang Range, *G. Forrest 22399* (E, UC, US, W); N of Lichiang, to Yungning, *F. Handel-Mazzetti 7029* (E, LE, W); Jingdong, *K. H. Hsue 5415* (NAS); Kunming, *T. N. Liou 17102* (PE); Yunnan Hsien, *E. E. Maire 203* (E); Tong-chouan, *E. E. Maire 7683* (NY, UC, US); between Kunming ("Yunnan-fu") & I-pin ("Suifu"), *R. Mell in 1914* (W); Tse-kou, *Monbeig s.n.* (E, NY, P, US); vicinity of Lichiang, *C. Schneider 3232* (G, GH, US); Kunming ("Yunnan-fu"), *O. Schoch 306* (US); Lan-ping Hsien, *H. T. Tsai 54053* (NAS); Lenping Hsien, *H. T. Tsai 54012* (A, PE), *54083* (A, PE); Chi-tye-lo Hsien, *H. T. Tsai 58180* (NAS); Chong-shan, Tali, *Y. Tsiang 11572* (NAS); Wei-hsi Hsien, Yeh-chih, *C. W. Wang 68166, 62271* (A); Weisi Hsien, *C. W. Wang 64568* (PE), *67667* (A, PE), *67687* (PE), *67969* (A, PE), *68679* (A, NAS, PE), *68271* (PE), *68369* (A, PE), *68679* (NAS, PE); Chinatung, *C. W. Wang 65191* (NAS); Gongshan Hsien, *C. W. Wang 67210* (PE); Deqem Hsien, *C. W. Wang 67667, 68166, 68863* (PE), *69214, 69864* (A, PE); Huann-fu-ping, A-tun-tze, *C. W. Wang 69214* (NAS); Chen-k'ang, Snow Range, *T. T. Yü 17045* (A, E); Chiang-ch'uan, Buhlaka (Chulung), *T. T. Yü 19582* (A, E); Likiang, *S. W. Yu 64-045* (KUN); Zhongdian, *Zhongdian Exped. 849* (PE). ZHEJIANG: Taihua Shan, *K. K. Tsoong 2213* (PE).

INDIA. ASSAM: Khasi Hills, Mawphlang, *R. Chand 2274* (MICH), *7978* (DS, MICH); Khasi Hills, Tsillong, *C. B. Clarke 5815* (BM); Shillong, *C. B. Clarke 38753* (G); Naga Hills, Kohina, *C. B. Clarke 40987* (BM); Khasi Hills, *J. D. Hooker & T. Thomson s.n.* (BM, G, L, LD, S, UPS, W); Khasi Hills, Shillong, *F. Kingdon-Ward 18675* (A, BM); Khasi Hills, Laitlynkot, *W. Koelz 23114* (DS, MICH), *23328* (DS, MICH); Khasi Hills, Mawryngkneng, *W. Koelz 28318* (DS, MICH). WEST BENGAL: Darjeeling, Phalut, *H. Hara et al. in 1960* (TI); Darjeeling, Sandakphu, *A. K. Skvortsov in 1972* (MO). HIMACHAL PRADESH: Manali, *U. C. Bhattacharyya 44746* (TI); Dalhousie, *C. B. Clarke 22381* (BM); Simla, *J. Drummond in 1884* (G); between Dalhousie & Chamba, *J. Duthie 18038* (UC, W); Mahasu, *Fleming in 1849* (E); Simla, *Harmand s.n.* (P); Chamba, *J. H. Lace 1855* (E); Simla, *R. N. Parker 3357* (GH); above Simla, *L. Ram 1585* (E); Kotgarh, *Stoliczka s.n.* (W); Simla, *G. Watt in 1887* (E); Jalanri Pass, near Simla, *G. Watt 9614* (E). KERALA: Kottayam Dist., Petimudi-Devicolam, *B. V. Shetty 26584* (MH). MADRAS: Palni Hills, *R. H. Beddome 3145, 8226* (BM); Anamalai, *R. H. Beddome 8227* (BM); Madurai Dist., Vattakanal, *D. B. Deb 30968* (MH); Nilgiri Dist., Tamilnadu, Mukurti, *J. Ellis 43413* (MH); Palni Hills, *M. A. Evershed s.n.* (BM); Nilgiri Hills, *M. Perrottet in 1837–1838* (G); Nilgiris, *R. J. Shuttleworth s.n.* (BM); Nilgiri Mts. & Kurg, *G. T. s.n.* (GH, L, P, W); Nilgiri Hills, *M. Wight in 1841* (E), *M. Wight 94* (G). MANIPUR: Ukhrul, *F. Kingdon-Ward 17976* (BM, NY). PUNJAB: Hathu above Simla, *J. Drummond 1586* (UC); Kunawar, *J. Drummond 22331* (UC). WEST PUNJAB: Kulu, Nandukital, *W. Koelz 1442* (MICH, NY); Dalhousie, *W. Koelz 8879* (NA, NY). SIKKIM: Lachung, *G. A. Gammie 670* (E); Reg. temp., 9–12,000 ft., *J. D. Hooker s.n.* (GH, S); Lachung, *Rhibu & Rhomoo 5567* (E). UTTAR PRADESH: Mussooree, Jabberkhet, *A. Anderson in 1920* (E); Pindar Valley, Garwhal, *G. E. Bentham in 1924* (BM); Tihri, Garhwal, Lekhun Gidh, Sri Kanta Mt., *J. F. Duthie 1049* (G), *1049a* (E, G); Chakrata, *B. Kaur in 1958* (G); Kandia, Tehri, *W. Koelz 21719* (NA, NY); Chakrata, Chilmiri-Neck, *K. Maheshwari in 1958* (E); Deoband-Kanasar Road, Jaunsar, *M. B. Raizada 7181* (DS, E); Jabberkhet, Mussooree, *R. R. Stewart 11199* (MO, NA, NY, PENN), *16742* (US); Kumaon, *R. Strachey & J. E. Winterbottom 1* (GH); Kumaon, Saba, *R. Strachey & J. E. Winterbottom 2* (BM, GH); Kumaon, Binjar, *R. Strachey & J. E. Winterbottom 3* (BM, GH). STATE UNKNOWN: Chimili Valley, *A. Anderson? 1198* (E); Chandanwari, *H. Heybroek 53* (L); Bear Khola, Kodaikanal Hills, *K. C. Jacob 16172* (MH); "India," *V. Jacquemont 739, 2364* (P); Lachul, Kokhsar, *W. Koelz 695* (MICH, NY); pass above Lubbie, *J. R. Reid? in 1885* (E); Garkanda, *Stoliczka s.n.* (W); Himal. Bor. Occ., *T. Thomson s.n.* (BM, G, GH, GOET, L, LD, NY, P, W).

KASHMIR. Lahnarg, *J. H. Barbour in 1922* (BM); Kunshwan, *C. B. Clarke 29471* (BM); vicinity of Pahlgam, 27 mi. N of Islamabad, *F. G. Dickason 763* (MICH); vicinity of Sonamarg on the Sind R., *F. G. Dickason 764* (MICH); Astor Dist., above Doyen, *J. F. Duthie 12474* (E); Liddar Valley, *J. F. Duthie 13064* (BM, E); Pahlgam, *M. A. Evershed in 1913* (BM); above Tarakbal, *W. Koelz 9186* (NA, NY); Pahlgam, *N. C. Nair in 1966* (NCU); Azad, above Chikar, *E. Nasir 1027* (E); Khelanmarg, *O. Polunin 56/145* (BM); Ferosopae Nullah?, *P. Purfold 232* (BM); Huzzaffarabad, Deepa Valley Road, *M. Qaiser & A. Ghaffar 5009* (KUH); Pahlgam, *A. K. Skvortsov in 1972* (MO); Koraghal, N slope Rajdhiangan Pass, *R. R. Stewart in 1946* (W); Tragbol, *R. R. Stewart 4827* (PH); Padar, upper Chenab, *R. R. Stewart 3075* (NY); Keran, Kishen Ganga valley and road to Nanga Parbat via Gangbal Lakes, *R. R. & I. D. Stewart 17604* (NY, UC, US); Astor Dist., Rupal Nullah, *R. R. Stewart 22852* (NY).

NEPAL. Kalingchok, *Banerji Herb. in 1964* (A); Sunderijal Reservoir, 8 mi. NE of Kathmandu, *D. D. Bhatt 41* (UC); Sheopuri, N of Kathmandu, *C. Chuma in 1970* (TI); Suli Gad, *Einarsson et al. 3200* (BM); Bilbatay, Bhanjang, above Tutay, *H. Hara et al. 6300557* (KYO, TI); Hati Sar-Mangal-

bare-Lam, Phokari-Minchin Dhap, *H. Hara et al. 6300558* (BM, KYO, TI); Taplejung-Heydewa-Bunklung, *H. Hara et al. 6300559* (TI); Singalila, Kalapokhari, Sandakphu, *H. Hara et al. 69918* (TI); Phulchoki, S of Kathmandu, *H. Kanai 424* (KYO, TI); Sim Rhanjang, *H. Kanai 673313* (KYO, TI); Hilay Dhap, *H. Kanai & Malla 674737* (TI); Dor-tute, *H. Kanai et al. 872272* (TI); Mul Kharka, Chipu Danda, *Malla & H. Kanai 673496* (TI); Tolo Gompa Khola, *S. Nakao & J. H. E. 195* (KYO); Maharigaon, *O. Polunin et al. 168* (BM); Jumla, *O. Polunin et al. 382* (E, G, UPS); Langtang, *O. Polunin 1646* (BM); Chutta, SE of Jumla, *O. Polunin et al. 4921* (BM, E, UPS); N of Taplejung, Thapabu Khola, *J. D. A. Stainton 1179* (BM); Gurjakhani, *J. D. A. Stainton et al. 3564* (E, UPS); Chimgaon, N of Tukucha, Kali Gandaki, *J. D. A. Stainton et al. 7831* (BM, E); Lete, S of Tukucha, Kali Gandak R., *J. D. A. Stainton et al. 7873* (BM); Milke Bahnjyang, *L. H. J. Williams 1097* (BM).

PAKISTAN. Chitral above Shagram, Kagan Hills, *L. Ali & F. Grohmann 5995* (RAW, US); Abbottabad ("Hazara"), Hill Terr., between Chail Sar & Ganja Kandao, *B. L. Burt & M. A. Kazmi 1240* (E); Abbottabad, Nilishang Terr., Khator to Sharkul, *B. L. Burt & M. A. Kazmi 1328* (E); Kankoli, Kagan Hazara, *J. Duthie in 1899* (CAS); Kao Forest, *D. McVean in 1960* (E); Swat, Jaba, *E. Nasir 3941* (RAW); Murree, *E. Nasir & Y. Siddig 29162* (RAW); Islamabad, Changla Gali, Murree Hills, *Y. Nasir 70* (MO); Hazara Dist., Thandiaru, *Y. Nasir 6154* (RAW); Swat Dist., Jabber, *M. Qaiser & A. Ghaffar 4822* (KUH); Swat State, between Maina & Ilam Mt., *R. J. Rodin 5466* (G, UC, US); Hazara Dist., Mohshpuri, *M. A. Siddigi & Y. Nasir 5991* (RAW); Changla Gali, Murree Hills, *R. R. Stewart in 1949* (PH, US), *4103* (MO, NY); Swat State, Utrat, *R. R. Stewart & A. Rahman 15153a* (BM); to Bantara Gali, *R. R. Stewart & E. Nasir 24089* (RAW).

VIETNAM. Tonkin, Cha Pa, *M. Petelot 3065* (P, UC), *3065A* (NTUF).

Circaea alpina subsp. *imaicola* is distinguished by the flowers being held on erect or ascending pedicels and opening before elongation of the raceme, the pubescent (at least sparsely) stem, deep green or bluish-green opaque leaves, and the ovate to very broadly ovate leaves with usually rounded or truncate bases. A minute bracteole is present at the base of the pedicel. Although the vast majority of plants have subentire to minutely denticulate, pubescent leaves, some have leaves approaching *C. alpina* subspp. *alpina* and *micrantha* in shape and toothing. *Circaea alpina* subsp. *alpina* always has glabrous stems and those of *C. alpina* subsp. *micrantha* are usually glabrous. Both of these subspecies also have thinner, translucent leaves and softer petioles that are flattened and often appear winged in pressed specimens. Numerous specimens of *C. alpina* subsp. *imaicola* have the ovaries glabrous at maturity. Among these are *Monbeig*, Tsékou (E, NY, P), *Smith 10948* (S, UPS), *Forrest 6332* (BM, E), *Forrest 6338* (BM, E, P), *Tsai 54012, 54083* (A), *Delavay 6533* (MO, P), plus many others. The collections of *Ludlow, Sherrff* and *Elliot 15583* (BM, E) have prominently toothed leaves as in *C. alpina* subsp. *micrantha* but are noncordate as in subsp. *imaicola* and the flowers and stem pubescence are like subsp. *imaicola*. *Wang 69079* (A) has lightly pubescent stems, glabrous ovaries at anthesis, a densely glandular inflorescence axis, prominently toothed leaves that are cordate at the base, but petals notched more than one fifth of the way to the base and represent plants intermediate between *C. alpina* subspp. *imaicola* and *micrantha*. These plants appear to be fully fertile, having normal fruit set.

In general, *Circaea alpina* subsp. *imaicola* grows at lower elevations than subsp. *micrantha* (Skortsov, 1977) but there is a considerable area of overlap between 3,000 and 4,000 meters. Plants of *C. alpina* subsp. *imaicola* often, but not always, tend to resemble subsp. *micrantha* to a greater degree as elevation increases.

7d. Circaea alpina L. subsp. **pacifica** (Asch. & Magnus) Raven, in Calder & Taylor, Canad. J. Bot. 43: 1396. 1965.—FIG. 22.

Circaea pacifica Asch. & Magnus, Bot. Zeitung (Berlin). 29: 392. 1871.
Circaea alpina L. var. *pacifica* (Asch. & Magnus) M. E. Jones, Bull. Univ. Mont. Biol. ser. 61: 39. 1910.
Circaea alpina L. forma *pacifica* (Asch. & Magnus) G. N. Jones, Univ. Wash. Publ. Biol. 5: 195. 1936.

Plants (1.0–)1.5–3.5(–5) dm tall. Stem densely to very sparsely pubescent, at least on the uppermost internodes or at the nodal areas, with soft, short, falcately recurved hairs, 0.1–0.2 mm long; the petiole glabrous to densely pubescent with hairs as on the stem but upwardly curved; the leaves glabrous or with similar, upwardly curved hairs along the veins, rarely on the interveinal areas near the base, on the upper surface; the inflorescence densely to sparsely pubescent with short glandular hairs. The stem, and less often the petioles, firm terete, remaining mostly unflattened in pressing, or the petioles flattened, and appearing winged. Stem green, very rarely the nodes purple. Leaves pale green, translucent; those near the summit of the stem, and most often the second pair below the inflorescence, the largest, 3–7.5(–11) cm long, 2–5.5(–8) cm wide; abruptly reduced upward and rapidly becoming bractlike at the base of the inflorescence, gradually or, rarely, abruptly reduced downward, only rarely a few pairs of leaves near the summit of the stem clustered and appearing somewhat whorled. Leaves ovate to broadly so, rarely subcircular, acute to very short acuminate at the apex, rounded to subcordate, very rarely cordate, at the base, subentire to denticulate; glabrous or with sparse, falcate hairs, 0.1–0.2 mm long on the main veins above and, less commonly, on the interveinal areas near the base, also with slightly curved to falcate cilia along the margins. Petiole 1.5–3(–5) cm long, subterete to terete, glabrous to densely pubescent, at least in lines along the upper surface, with short, soft, upwardly curved, falcate hairs, 0.1–0.2 mm long; with or without reduced branches arising in the axils. Inflorescence sparsely to, more commonly, densely pubescent with short, soft, capitate and clavate-tipped glandular hairs 0.1–0.2 mm long; terminal on the main stem and at the tips of the uppermost axillary branches, very rarely at the tips of axillary branches arising from the base of the stem in some dwarfed individuals. The inflorescence simple or, more commonly, with alternate or opposite lateral racemes from the base, these subtended by leaflike bracts, less commonly by reduced leaves. Flowering pedicels glabrous, 0.9–2.3 mm long, ascending or erect; the flowers clustered at the apex and opening before elongation of the raceme; with or without a minute bracteole at the base, when present, to 0.2 mm long. Fruiting pedicels (1.8–)2.3–4.2(–5) mm long. Buds glabrous, broadly elliptic to oblong obovate or narrowly to broadly obovate in outline, obtuse or minutely mammiform at the apex; from the summit of the ovary 1.5–2.2(–2.6) mm long, 0.6–1 mm thick; white. Ovary 0.5–1.1 mm long, 0.3–0.6 mm thick at anthesis, clavate to slenderly so, pubescent with soft, short, translucent, uncinate hairs. Floral tube 0.3–0.5(–0.6) mm long, 0.2–0.3 mm thick at the narrowest point, broadly funnelform. Sepals 1–1.7(–2.1) mm long, 0.6–1.1 mm wide, white, oblong ovate to oblong obovate, rounded to the obtuse or minutely mammiform apex. Petals (0.8–)1–1.6 mm long, 0.7–1.3 mm wide, longer than wide, white, obovate to obdeltoid in outline; the apical notch 0.2–0.5 mm deep, ¼–⅓ the length of the petal; the petal lobes rounded. Filaments 0.8–2 mm long; anthers 0.3–0.4 mm long, 0.2–0.3 mm thick. Style 1.3–2.2 mm long; stigma 0.1–0.2 mm tall, 0.3–0.4 mm thick. Mature fruit clavate, rounded at the

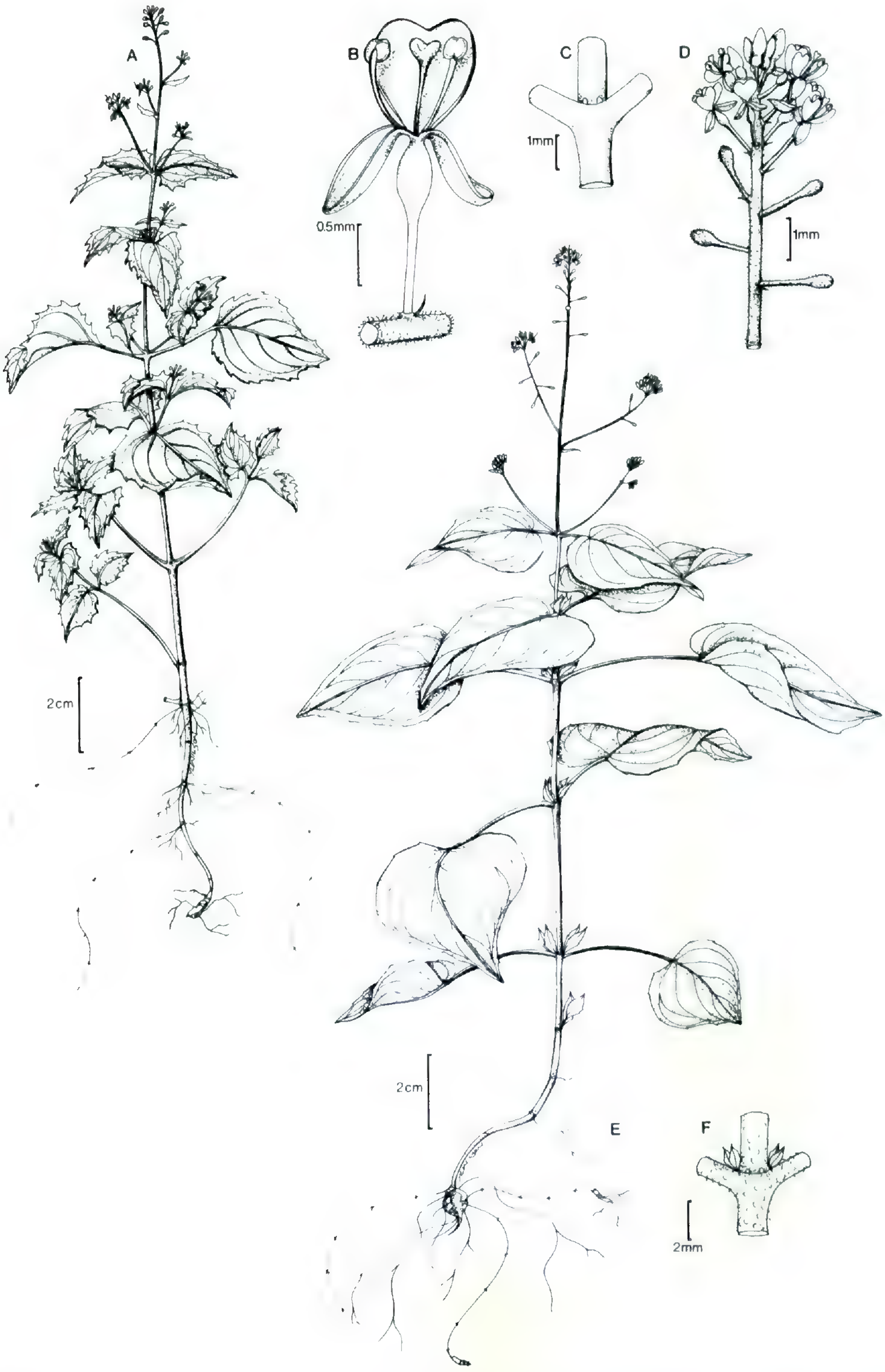


FIGURE 22. *Circaea alpina* L. subsp. *micrantha* (Skvortsov) Boufford.—A. Habit.—B. Flower with petal removed.—C. Node of stem.—D. Inflorescence. From *Ludlow et al. 5106* (E). *Circaea alpina* L. subsp. *pacifica* (Asch. & Magnus) Raven.—E. Habit.—F. Node of stem. From *Harris & Harris, Pl. Exs. Grayanae 672* (MO).

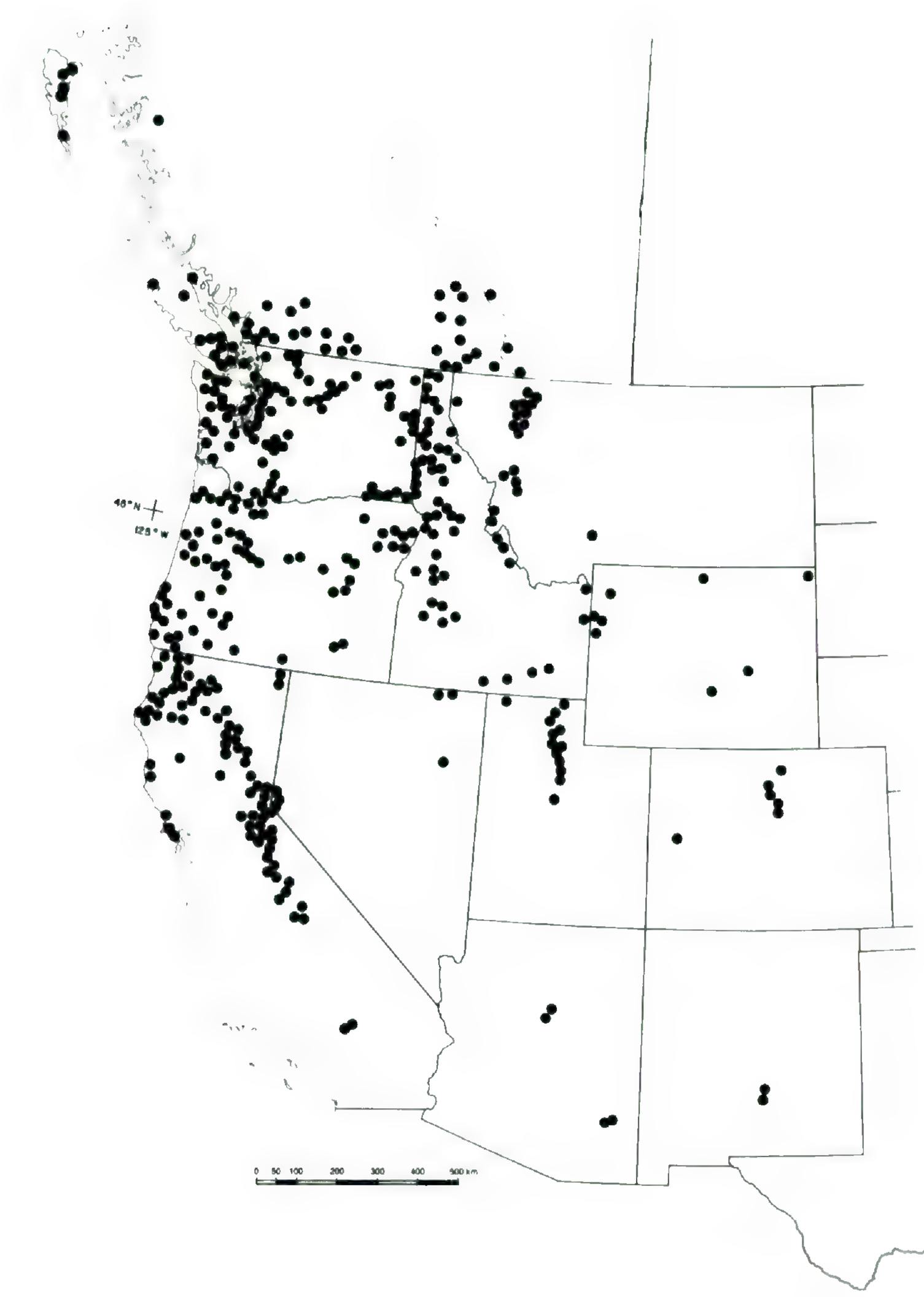


FIGURE 23. Distribution of *Circaea alpina* L. subsp. *pacifica* (Asch. & Magnus) Raven.

apex, 1.8–2.2(–2.5) mm long, 0.6–1.2 mm thick, the translucent uncinate hairs 0.3–0.5 mm long. Combined length of pedicel and mature fruit (3.5–)4.2–5.5(–6.5) mm long. Gametic chromosome number, $n = 11$.

TYPE: Munz (1965) gives as the type locality "Near San Francisco California." This can probably be interpreted as a designation of Bolander's collection, cited by Ascherson and Magnus (1871) in their original description, as the lectotype. However, I have been unable to locate any of Bolander's specimens.

Distribution (Fig. 23): Cool moist coniferous forests. From the San Bernardino Mountains in southern California north to central British Columbia, eastward to the Rocky Mountains and southward in the mountains to New Mexico and Arizona. From near sea level, in the northwestern part of the range, to 2,700 m. Flowers, May to mid-August.

Representative specimens examined:

CANADA. ALBERTA: Summit Lake, *G. Armstrong & J. Nagy 5033* (ALTA, CAN); Waterton Lakes National Park, Bertha Creek, *A. J. Breitung 17416* (ALTA, RSA, SMU); Waterton Lakes, trail to Bertha Lake, *A. J. Breitung 16214* (NY), *M. Malte & W. Watson 2624* (UAC, WTU), *R. T. Ogilvie in 1960* (UAC, UBC), *K. Shaw 2855* (BRY); Cameron Lake, *G. N. Jones 23915* (COLO, ILL), *J. Ewan 18496* (NO, RSA); Waterton Lake, *F. Hermann 13072* (ALTA, US); E slope of Mt. Crandell, *J. Kuijt & D. R. Dobbins 4434* (SMU); Crowsnest area, Upper Carbondale Valley, *R. T. Ogilvie in 1960* (UBC); Castle R. region, *R. Cormack in 1944* (ALTA); Castlemount, 8 mi. up W Branch of Castlemount R., *M. Malte & W. Watson 2505* (UAC); between N Kootenai Mt. and Lynx Creek Campground, *J. Parker & G. Silberhorn 1971-138* (ALTA). BRITISH COLUMBIA: Vancouver Island, Nanaimo District, Goldstream, *J. Anderson in 1908* (V, WS), *J. Anderson 152* (V), *J. W. Eastham in 1939* (UBC); Goldstream Provincial Park, *J. Bailey 7161* (V); Nanaimo, Discovery Bay, *A. Eastwood 9890* (CAS); Cowihan Lake, Robertson Creek, *J. Anderson in 1916* (V, WS); vicinity of Nanaimo, *J. Macoun in 1908* (CAN, NY); along the San Juan R. E of Port Renfrew, *J. A. Calder & K. T. Mackay 30922* (DAO, DS, MAK); W Nanaimo R. valley, *D. Mueller-Dombois 11-25* (UBC); head of Finlayson Arm, N of Victoria, *J. A. Calder & K. T. Mackay 31516* (DAO); Alberni, Roger Creek, *W. R. Carter C405* (POM, V); Loman R., *W. R. Carter 10H1* (UBC); Westholm, Eves Park, *N. Chapman 243* (V); Sooke Harbour, *G. Copley 350* (V); Cowichan Lake, near Shaw Creek, *S. Ewan & L. Pugsley 126* (V); Green Mt., *S. Ewan & G. Pugsley in 1973* (V); Strathcona Provincial Park, *S. Kojima in 1969* (UBC); Macmillan Park, 187 mi. N, *V. Krajina & R. H. Spilsbury 4879* (UBC); between 3rd & 4th Nanaimo Lakes, *V. Krajina et al. 5315* (UBC); Macmillan Park, *V. Krajina et al. 5340* (UBC); Saanich, *W. Newcombe 8830* (V); Sooke District, Coal Creek, *C. Newcombe in 1894* (V); Cowichan District, *W. Newton in 1929* (DAO); Kyuquot, Kaouk R., *T. M. C. Taylor & A. F. Szczawinski 314* (UBC, V); Saltspring Island, Mt. Tuam, *T. R. Ashlee in 1957* (UBC); Fraser River delta, Burns Bog, *K. I. Beamish 680155* (UBC); 9 mi. N of Squamish on Paradise Valley Road, *K. Beamish et al. 610191* (CAN, UBC); Kaslo, *M. Bell in 1960* (UBC); Flathead District, Calvin Creek, *M. Bell & J. Davidson 863* (DAO, UBC, V); Anvil Island, N side, *W. Bird 4088* (UBC); Hope, *T. C. Brayshaw 49207* (UBC); Quadra Island, from Heriot Bay to Granite Bay, *J. A. Calder & K. T. Mackay 30050* (DAO); 6 mi. SE of Nakusp, *J. A. Calder & D. Savile 9981* (DAO); N of W Creston, *J. A. Calder & D. Savile 9327* (DAO); 7.5 mi. SW of Cheam View on Hope-Vancouver Hwy, *J. A. Calder & D. Savile in 1953* (DAO); Graham Island, Yakoun R. bridge SW of Port Clements, *J. A. Calder & D. Savile 35560* (B, DAO, H, V, W); ca. 4.5 mi. S of Port Clements, *J. A. Calder et al. 35038* (DAO); Cultus Lake, *C. Carl 13756* (V); near Quamichan Lake, Duncan, *D. Charter 129* (UBC); Manning Park, Castle Creek, *C. C. Chuang 525* (CAN, UBC, V); Manning Park, Grainger Creek, *C. C. Chuang 1279* (V); Mayne Island, *J. Davidson in 1915* (UBC), *J. Macoun 238* (V); Whiterock, *J. Davidson in 1916* (UBC); Nelson, Ymir R., *J. W. Eastham in 1937* (UBC); Erickson, *J. W. Eastham in 1938* (DAO, UBC); W Langley, *J. C. Ellens in 1960* (NCU, V); ca. 2.5 mi. SW of Rosedale, *D. Faris, Jr. 94* (DAO, UBC, V); Hope-Princeton area, *F. Fodor in 1938–1945* (UBC); Salt Spring Island, Ganges, *V. Goddard in 1935* (V); 9 mi. NW of Oliver, *J. Grant 62-35* (DAO); Otter Road near Langley Prairie, *H. Groh s.n.* (DAO); Manning Park, *G. Hardy 21726* (V); Kamloops District, Celista, N side of Shuswap Lake, *G. Hardy in 1952* (V); near Vancouver, *J. K. Henry 4242* (RM); Kokanee Park, *B. Herbison WK73419A* (V); Borser Island, *A. Hill in 1897* (UBC); Spanish Banks, *L. Holm 405* (UBC); Shawnigan Lake, *F. Hunnewell 7835* (GH); Lytton, *V. J. Krajina in 1949* (NCU, UBC, WTU); Paradise Valley, *D. L. Krause 3067* (UBC); Griffin Island, *J. Macoun 677* (CAN, DAO, US); Rocky Mts., Cannore, *J. Macoun 2020* (CAN); Chilliwack R., *J. Macoun 44409* (CAN, WS); Columbia Valley, Donald, *J. Macoun in 1885* (MTMG, NY); 40 mi. E of Bella Coola, *T. T. McCabe 1531* (UC, WTU); Silver Creek, *T. T. McCabe 2474* (UC); Alta Lake, Sproat Mt., *T. T. McCabe 2984* (UC); Sumas Mt., Sumas Prairie by McKay Creek, *T. T. McCabe 3614* (UC); E side of Kootenay Lake, *W. McCalla 8325* (ALTA, V); Cheakamis R. Road, 1–2 mi. above Fergie's Lodge, *W. H. Parker 152* (DAO, UBC); 6 mi. NE of Rosedale, *H. Senn et al. 5824* (DAO); Salmo, *J. Shoustoff 44* (V); Glacier National Park, Couger Valley, *A. F. Szczawinski in 1964* (UBC, V); near Moyie R., Tochty, *R. L. Taylor & D. H. Ferguson 2861* (DAO, DS); Galena, *T. M. C. Taylor & A. F. Szczawinski 526* (UBC); Victoria, *J. Tolmie in 1897* (DAO); Armstrong, Okanagan, *E. Wilson s.n.* (UBC); Selkirk Mts., N Fork Illecillewaet R., *J. MacMillan 564* (MO); Upper Loop Creek Valley, Glacier, *E. W. D. Holway in 1914* (MIN); Illecillewaet Valley, *S. Brown 660* (CAN, MO, PH, US); Queen Charlotte Islands, Graham Island, Mamin R. delta at Juskatla, *R. L. Taylor 133* (DAO); Honna R., Skidegate Inlet, *R. Pillsbury 357* (UBC); ca. 2 mi. W of Queen Charlotte City, *J. A. Calder et al. 34802* (DAO); Moresby Island, Copper Creek 3 mi. S of Copper Bay, *J. A. Calder et al. 21885* (DAO); Queen Charlotte City, near bridge over Honna R., *J. A. Calder & R. L. Taylor 36934* (B, COLO, DAO, DS, MAK, NCU, RSA, TUR, UC, WS, WTU); Mt. Cheam, *F. Anderson in 1899* (DAO).

UNITED STATES. ALASKA: Juneau, *E. Shumway in 1890* (GH). ARIZONA: COCONINO COUNTY, Oak Creek Canyon, Coconino National Forest, *D. Demaree 41261* (ASU), upper Oak Creek, *H. J.*

Fulton 9673 (ARIZ); GRAHAM COUNTY, Graham Mts., Swift Trail Road, *B. Maguire 12121* (BRY, DAO, GH, RM, UC, UTC, WS, WTU), Mt. Graham, *R. Peebles et al. 4482* (NA, US), Wet Canyon Campground in Pinaleno Mts., *Moore, Pinkava & Lehto L6348* (ASU, NCU, OS, UNCC), *R. A. Darrow 1052* (ARIZ), *S. Bingham 1555* (ASU). CALIFORNIA: ALPINE COUNTY, near Douglas Station, *R. Hoover 2602* (UC), Stanislaus Forest, Iceberg Meadow Ranger Station, *W. W. Eggleston 9560* (US); AMADOR COUNTY, 2.5 mi. W of Blakely, *C. Belshaw 2416* (UC), Panther Creek, *G. Hansen 272* (DS, MO), Mokelumne R. and tributaries, Deer Creek, *G. Hansen 272* (NY), Tiger Creek, *G. Hansen 272* (US); BUTTE COUNTY, first summit, Oroville-Quincy, *L. Benson 3962* (ND, POM), Jonesville, *E. B. Copeland 386* (ARIZ, CAS, CU, DS, GH, H, MICH, MO, NY, ORE, RM, RSA, UC, US, W, WIS), neighborhood of Jonesville, *H. F. Copeland 428* (DS, OKLA, POM, WIS), Butte Meadows, *A. A. Heller 14687* (DS, MO, NY, US, WTU), 3 mi. SE of Butte Meadows, Paynes Creek, *P. Johannsen 942* (UC); CALAVERAS COUNTY, San Antonio Creek, *W. Dudley in 1906* (DS), 1.2 mi. NE of Dorrington Ranger Station, hwy 4, *P. C. Everett & E. K. Balls 22024* (NY, RM, RSA, WS), Big Trees, *J. Hawthorne & F. Blaisdell in 1899* (CAS), Snowden Ranch, near Calaveras Big Trees, *W. L. Jepson 14388* (JEPS), near Calaveras Grove of Big Trees, *W. McCalla 6215* (ALTA); DEL NORTE COUNTY, Requa and vicinity, *E. McGregor in 1921* (DS), Siskiyou Mts., Mill Creek, *L. R. Abrams 8469* (DS); ELDORADO COUNTY, Sly Park, *H. M. Hall 11295* (CAS), Lake Tahoe, Emerald Bay, top of Eagle Falls, *J. T. Howell 1272* (CAS), Pyramid Peak, *Brewer 2133* (UC), S Fork American R., *H. M. Hall & H. P. Chandler 4761* (CM, UC), Glen Alpine Canyon, *L. R. Abrams 12701* (DS, HG, MO, NA, NY, POM, UC, WTU), Cosumnes, *G. Hansen 1909* (NEB), from Fallen Leaf Lake to Lake of the Woods, *F. Peirson 6298* (RSA), S edge of Fallen Leaf Lake, *P. H. Raven 21436* (DS, RM, RSA, TEX), 3 mi. E of Camino, *G. Robbins 1141* (CAS, UC), near Lily Lake, *G. L. Smith 2300* (JEPS), Glen Alpine Spring, *G. L. Smith 3304* (JEPS), Camp Sacramento, *W. Vortried in 1925* (CAS), Lake Tahoe region, from Fallen Leaf Lake, *I. Wiggins 6770* (DS, ND), ca. 4 mi. N of U.S. hwy 50 junction on road to Emerald Bay, Lake Tahoe, *H. M. Wheeler 443* (JEPS, WTU); FRESNO COUNTY, Pine Ridge, *H. M. Hall & H. P. Chandler 214* (CM, DS, MIN, MO, NY, PH, UC, US), Huntington Lake, *A. Grant 1148* (CU, DS, JEPS), King's R., Sharp Creek near Cedar Grove Camp, *P. A. Munz 15917* (CAS, GH, MONTU, POM, UC, WTU), 1 mi. S of Kaiser Diggings, *C. H. Quibell 182* (RSA), Snake Camp, 2 mi. N of Shaver Lake, *C. H. Quibell 3838* (NCU, RSA), *C. H. Quibell 3942* (RSA), bank of Sheep Thief Creek, junction of Stump Springs Road and 168, *M. & H. Quibell 3544* (RSA), Daulton Road directly opposite Brown Cone, *C. H. Quibell 290* (RSA), Sequoia Mills, *A. Eastwood in 1893* (MIN), Horse Corral, *Mrs. J. Clemens in 1910* (POM), upper branch of Round Meadow, *E. Carter 5828* (RSA), Stump Springs Road, *L. Beane 1592* (DS); GLENN COUNTY, Plaskett Meadows, *J. T. Howell 19010* (BH, CAS); HUMBOLDT COUNTY, hwy 299 E of Blue Lake, *D. E. Anderson & J. P. Smith J-1101* (WS), Klamath R., *H. P. Chandler 1404* (CM, DS, GH, MIN, MO, NY, PH, RM, UC, US), 5 mi. W of Dyerville, *L. Constance 742* (WS), near Dinsmore's, *A. Eastwood & J. T. Howell 4780* (CAS), E of Bridgeville on hwy 36, *W. J. Ferlatte & B. D. Rogers 2095* (COLO, H, NLU, SMU, WIS, WTU, WVA), Yager Creek at 2,400 ft, *C. C. & S. K. Harris Pl. Exsic. Grayanae 672* (ARIZ, BH, BHO, CAN, CAS, COLO, CU, DAO, DS, DUKE, GA, GH, IA, ILL, IND, ISC, KANU, LL, MASS, MICH, MIN, MO, MONTU, NA, NCSC, NCU, NHA, NO, NY, OKLA, PAC, PENN, PH, POM, RM, SMU, TENN, TEX, TRTC, UC, UNCC, US, UTC, WIS, WS, WTU, WVA), Chapanal Mt., Bug Creek, *D. K. Kildale 3766* (BH), Lawrence Creek, *D. K. Kildale 835* (DS), Van Duzen, *A. R. & H. N. Moldenke 24876* (LL), 5 mi. N of Willow Creek on Racoon Creek, *P. A. Munz 16552* (OKLA, RSA, WTU), 1.1 mi. S of Friday Ridge Road on Titlow Hill Road, near Grouse Mt., *P. H. Raven & R. Snow 13640* (CAS, RSA), Yances Camp, *H. Smith 3909* (US), near Hydesville, Wolverton Gulch, *J. P. Tracy 2441* (UC), Lawrence Creek at crossing on the Kneeland Road, *J. P. Tracy 6691* (UC), Four Mile Creek on Friday Ridge Road, W of mouth of S Fork Trinity R., *J. P. Tracy 15381* (UC, TEX), valley of Van Duzen R. opposite Buck Mt., *J. P. Tracy 2716* (BRY, NCU, UC), along Willow Creek, near its mouth, *J. P. Tracy 3311* (UC, US), South Fork Mt., near McKay Camp, *J. P. Tracy 8927* (UC), ridges E of Corral Prairie, *J. P. Tracy 10585* (UC), Grouse Mt., *J. P. Tracy 13459* (DAO, UC), Trinity Summit, lower end of Butte Hole, *J. P. Tracy 14159* (UC, WIS), head of Little Hors-Linto Creek, *J. P. Tracy 15088* (UC, UTC), Bear R., 10 mi. upstream from mouth, *J. P. Tracy 15349* (UC), 5 mi. W of Dyerville, *L. N. & G. B. Upton in 1930* (CU), 11 mi. E of Hoopa Valley on new road to Trinity Summit, *C. Wolf 9253* (DS, MT, NY, RSA, TEX, WTU); LASSEN COUNTY, Mt. Lassen National Park, 1 mi. below Drakesbad, *B. Cain* (DS); MADERA COUNTY, Westfall Campground just S of Fish Camp & Mariposa County, *Cook et al. 2033* (ASU), Miami Ranger Station, *L. R. Gillogly 20* (ARIZ, ND, POM, UC); MARIN COUNTY, near Camp Taylor, *E. Cannon in 1899* (CAS), between Bolinas & Olema, *A. Eastwood in 1898* (MIN, RM, UC), between Lagunitas & Camp Taylor, Lagunitas Creek, *H. M. Hall 8503* (ARIZ, CAN, DS, GH, NY, ORE, OSC, POM, RM, UC, US, WTU), Devil's Gulch near Camp Taylor, *J. T. Howell 24324* (CAS), Paper Mill Creek, *W. L. Jepson 8279* (JEPS), Bear Valley, *E. Zeile in 1911* (CAS), canyon behind Inverness Park, *B. Schreiber 920* (UC), Taylorville, *J. Moore 384* (CAS), *A. Edwards in 1878* (NY), Mt. Tamalpais, Redwoods, *H. Reed 267* (NCSC, UC, UTC), Point Reyes, *H. M. Pollard in 1936* (B); MARIPOSA COUNTY, Yo-

semite Valley, *E. F. Andrews in 1892* (AUA), along Merced R. in Little Yosemite Valley, *R. Bacigalupi 1849* (POM), 5 mi. SW of Yosemite Tunnel, *L. Benson 7703* (POM), Footman Mt., *J. W. Congdon in 1887* (MIN), Snow Creek, *J. W. Congdon in 1883* (MIN), Biledo Meadows S of the Mariposa Big Tree Grove, *D. B. Dunn 1940* (UMO), Yosemite, Little Crane Creek, *H. M. Hall & E. Babcock 3423* (DS, POM, RM, UC), Wawona Valley, *J. T. Howell 390* (CAS), Yosemite National Park, Happy Isles, *S. W. Hutchinson 1452* (NO), Grouse Creek, Yosemite to Wawona, *W. L. Jepson 4286* (JEPS), near summit of Chowchilla Mt., *C. Quick 45-41* (CAS), Yosemite National Park, Round Mt., *H. K. Pratt 24* (ISC), Vernal Falls, *J. Redfield 2390* (MO), S of Mirror Lake, *B. Schreiber 1702* (UC), Yosemite, near Tioga Road, *E. E. Stanford 1909* (RM); MENDOCINO COUNTY, Big River, *J. McMurphy 199* (DS, NY, US), 3 mi. up Ten Mile R., *F. Peirson 3789* (RSA), Van Damme State Park, *F. Peirson in 1941* (RSA), Van Damme State Park, Fern Canyon, *P. H. Raven & R. Snow 13669* (CAS, GH, RSA), SE of Albion, *H. Ripley & R. Barneby 6859* (CAS); MODOC COUNTY, Warner Mts., Cedar Canyon, Stow's Meadow, *F. H. Frost 66* (JEPS), Modoc National Forest, *R. Thomas & C. Tilforth 39175* (CAS), Parker Creek, *F. Payne 801* (CAS), Taylor Creek near Forestdale, *F. Nutting s.n.* (UC), *M. S. Baker in 1893* (JEPS, UC); NEVADA COUNTY, Donner Pass region, *H. M. Pollard in 1936* (B), Truckee, *C. F. Sonne in 1884* (UC), Summit, Soda Springs, *P. B. Kennedy 259* (RM, UC), *M. E. Jones 2761* (POM), Rucker Lake, *P. H. Raven 10060* (CAS), Bear Valley, *W. L. Jepson in 1898* (JEPS, MO), Evers Valley to Frog Lake, *J. T. Howell 18757* (CAS); PLACER COUNTY, Emigrant Gap, *M. E. Jones in 1882* (POM), Flume below Emigrant Gap, *F. A. MacFadden 12562* (BHO, CAS, IDS, NY), Lake Tahoe, Chambers Lodge, *L. Rose 44239* (TEX), under rocks on Mueller R., *C. F. Sonne in 1884* (CM), under rocks on Tucker R., *C. F. Sonne 116* (CM), Cisco, near to Iron Spring, *H. Walker 1454* (NMC, POM, UC), Tahoe Forest, base of Twin Peaks, *W. W. Eggleston 21658* (NY, US); PLUMAS COUNTY, near Lassen Buttes, *H. Brown 635* (DS, MO, NY, US), Prattville, *A. Coombs in 1906* (GH), Greenville, Forest Lodge, *A. Eastwood in 1927* (CAS), Quincy, *W. W. Eggleston 7633* (NY, US), Lassen National Park, upper Willow Lake, *G. Gillett 802* (CAS, JEPS), near Prattville, *J. T. Howell 2174* (CAS), Drakesbad, *J. T. Howell 35797* (CAS), NW of Willow Lake, *J. T. Howell 35856* (CAS, MAK), S of Quincy, *D. Keck 1641* (DS), headwaters of Clear Creek, *C. Quick 1342* (CAS), Quincy, Gansner Creek, *R. Weatherby 1451* (CAS, NY, RM, RSA, UC), 4th Water, Bear Creek, Middle Fork Feather R., *R. Weatherby 1654* (NY, RSA, UC), Meadow Valley, U.S. Forest Service Camp, *R. Weatherby 1678* (DS, RSA), Big Meadows, *R. Austin in 1880* (NA), Mill Creek, *R. Austin in 1877* (NY); SAN BERNARDINO COUNTY, San Bernardino Mts., Green Valley, *J. B. Feurge 1447* (POM), Lake Arrowhead, *E. Kline in 1924* (UARK), San Bernardino National Forest, along Snake Creek E of Lake Arrowhead, *L. DeBuhr et al. 670* (ISC), 1 mi. N of Heap's Peak, *C. Tilforth et al. 594* (DS, RSA), N of Crestline, *J. Roos 2728* (POM), Bluff Lake, *P. A. Munz 10693* (NY, POM, RM, RSA, UC), Little Bear Valley, *H. M. Hall 1000* (MO, UC), *H. M. Hall 1296* (NY), Bluff Lake, *G. Goodman & C. Hitchcock 1757* (ILL, MO, MONTU, NY), Strawberry Peak, *L. R. Abrams 2016* (DS, MO, NY, POM), Sawpit Canyon, W of Job's Peak, *J. Ewan 3546* (NO), *J. Ewan 5160* (CAS, DS, POM, UC), San Bernardino Mts., *S. & W. Parish 1158* (DS, ISC, MO, US); SHASTA COUNTY, E of Round Mt., Hatchet Creek, *L. Benson 2208* (DS, MO, NY, POM, UC, US), Hatchet Creek Summit, Hatchet Mt. on hwy 299, *V. & A. Grant 8000* (UC), Goose Valley, *A. Eastwood 881* (BH, CAS, GH), Lassen Volcanic National Park, 0.25 mi. above Manzanita Creek on Chaos Crags Trail, *G. Gillett 709* (CAS, JEPS); Sierra County, Pioneer Road Station, 2 mi. E of Bassett Station, N Fork Yuba R., *W. L. Jepson 16806* (JEPS), Girl Scout Camp near Bassett, *J. Kuijt 2372* (NCU, UBC); SISKIYOU COUNTY, Mill Creek, *L. R. Abrams 8469* (POM), Marble Mts., Sky High Valley, *A. Alexander & L. Kellogg 5874* (DS, MICH, MO, RM, UC, US, WTU), 1 mi. N of Forest Camp, Etna, *D. Barbe 061* (RSA, UC), Payne's Springs, *M. Baker 494* (UC), Shackelford Creek, *G. Butler 1499* (DS, POM, RM, UC, US), Klamath National Forest, Happy Camp to Waldo, Oregon Road, *A. Carter 706* (DS, GH, NY, UC), Mt. Shasta, along Mud Creek Dam road, *W. B. & V. G. Cooke 45455* (JEPS), W bank of Mud Creek Canyon, *W. B. Cooke 13860* (OSC), Mud Creek Canyon, *W. B. Cooke 15464* (NA, ND), near McCloud, *W. Dudley in 1899* (DS), Shasta Springs, *A. Eastwood 11030* (CAS), S Fork Salmon R. between campground and Carter's, *W. Ferlatte 1034* (RSA), T37N, R9W, Sec. 31, *W. Ferlatte 284* (RSA), near Jackson Lake, *E. Greene* (US), near Cudahy Lakes, *C. Hardham 13036* (RSA), NE base of Mt. Eddy, Metcalf's Ranch, *A. Heller 13251a* (CAS, DS, GH, ILL, MO, NY, PENN, PH, US, WIS, WTU), S Fork Salmon R. near Big Flat, *J. T. Howell 13367* (CAS), Marble Mts., Spirit Lake, *J. T. Howell 14982* (CAS), Little N Fork Salmon R. near mouth, *D. Kildale 5444* (DS), between Sawyer's Bar and Etna's Mill, *D. Kildale 5533* (DS), Elk Lick, S Fork Indian Creek, *D. Kildale 8754* (DS), beside Black Mt. at creek, *G. Muth 237* (RSA), Marble Mt. Wilderness Area, vicinity of English Peak, *F. Oettinger 480* (RSA, UC), Salmon Mts. Range, near Etna Creek, *D. Parker in 1949* (UC, WVW), ca. 6 mi. SE of Cecilville, *H. & J. Thomas 4410* (DS), near Donomore Meadow, just S of the Oregon state line, *R. Waring 298* (OSC), China Creek, *I. L. Wiggins 13469* (DS, NY, UC, WS), Etna Mills, *J. P. Young in 1921* (CU); SONOMA COUNTY, Guernville, *V. Rattan in 1877* (CAS, RSA); TEHAMA COUNTY, ca. 40 mi. NE of Chico along hwy 32, Soda Springs Campground, *G. Evans in 1963* (UTC), Bluff Falls, *J. T. Howell 36066* (CAS,

OSC), Deer Creek Pass, *A. R. & H. N. Moldenke 24832* (LL), Salmon Mts., Coffee Creek, *H. M. Hall 8529* (DS); TRINITY COUNTY, Trinity Mts., Morris Meadows, *A. Alexander & L. Kellogg 5515* (DS, RM, UC, US, WTU), 18 mi. NW of Weaverville, *E. Carter 645* (CAS), Mud Springs, Trinity Summit, *J. Davy & W. Blasdale 5775* (US), T37N, Sec. 7, Big Flat, *W. Ferlatte 706* (RSA), Coffee Creek, *H. M. Hall 8529* (RM, UC, US), Big French Creek near Cobbs, *L. B. Kildale 10184* (BH), above Forest Glenn, *P. A. Munz 14356* (POM), Big Flat, *L. Rowntree in 1937* (TEX), Carville, *E. Van Dyke in 1931* (CAS), ca. 14 mi. NW of Trinity Center, *E. G. Voss & T. F. Groesbeck 13067* (MICH, WTU), ca. 1.5 mi. S of Trinity Center, *Wagnon 1750* (RSA), South Fork Mt., 5.7 mi. S of Cold Spring Lookout, *C. B. Wolf 9169* (NY, RSA, TEX); TULARE COUNTY, Sequoia National Park, Giant Forest, *R. Bebb 336* (OKL), *K. Brandegee in 1905* (US), *A. Cronquist 2037* (MO, ND), *L. M. Newlon 15* (JEPS), below Mineral King, *Y. Winblad in 1937* (CAS), Crane Meadow, *E. Twisselman 10139* (DS), near trail from Soda Spring to Quaking Aspen, *C. Smith 1232* (JEPS, RM, UTC, WTU), 5.4 mi. from Posey on road to White River, *P. H. Raven et al. 14353* (RSA), Nelson on Tule R., *F. Peirson 2089* (RSA), vicinity of Mountain Lake, *W. Dudley 926* (DS), Thorp's Meadow, *W. Dudley 3014* (DS), vicinity of Mt. Moses, *W. Duncan in 1923* (DS); TUOLUMNE COUNTY, Brightman's Flat, *A. L. Grant in 1916* (CU, JEPS), Dodge Ridge Road, 3 mi. from Pinecrest, *V. F. Hesse 2285* (JEPS), ca. 3 mi. NE of Strawberry, *R. Kral 21756* (VDB), Hetch Hetchy, *H. Mason 632* (DS, GH, NY, UC), Smith Peak Trail from Mather, *H. Mason 2191* (POM, UC), Mather, Acherson Meadow, *P. A. Munz 7436* (POM), Leland Meadows, *C. Quick in 1930* (MO), near Cow Creek Guard Station, Sonora Pass Hwy, *C. Quick 40-87* (CAS), 3 mi. W of Pinecrest, Lair of the Golden Bear, *P. H. Raven 20332* (DAO, DS, RSA, US), 3.5 mi. above Pinecrest on road to Bell Meadows, Gooseberry Camp, *I. L. Wiggins 8997* (DS, RSA, WS). COLORADO: BOULDER COUNTY, Gregory Canyon, *H. W. Campbell 595* (COLO), Rangers trail to summit of Green Mt., *J. Ewan 11239* (CAS, GH, ND, RSA), Green Mt., Twin Springs, *J. A. Ewan 12250* (NO), *J. A. Ewan 12251* (CAS, RSA, UC, WS), N slope of Bear Mt. above Boulder, Fern Canyon, *J. A. Ewan 12078* (CAS, NO, RSA), Coal Creek Canyon, SW of Eldorado Springs, *J. A. Ewan 14379* (CAS, COLO, ILL, NO, RSA), SW corner of Boulder city limits along Royal Arch Trail, *E. Haber & D. R. Given 1997* (CAN, DS, SASK, V), 4 mi. SW of Boulder, *J. Murdock 424* (BRY), Boulder, *G. Osterhout 4631* (NY), 4–5 mi. SW of Boulder, *G. Robbins 786* (UC), mesa S of Boulder, *F. Ramaley 5099* (ORE); JEFFERSON COUNTY, Turkey Creek Canyon, *P. A. Munz 150* (CU), Golden, in Coal Creek Canyon, *Johnston & Hedgcock 395* (RM); LARIMER COUNTY, Fort Collins, *L. H. Pammel in 1896* (ISC); MESA COUNTY (?), Mesa, *W. W. Robbins in 1908* (COLO). IDAHO: ADA COUNTY, Boise, *J. F. Macbride 251* (GH, IA, MIN, MO, RM); BANNOCK COUNTY, Scout Camp, *R. J. Davis 152-35* (IDS), Chatcolet, *C. Coziero in 1904* (WS); BOISE COUNTY, Squaw Butte, *J. A. Clarke 271* (BH, CAN, DS, GH, MIN, MO, RM), ca. 3 mi. N of North Fork Boise R. on Little Owl Creek, *C. L. Hitchcock & C. V. Muhlick 10052* (CAS, DS, GH, NCSC, NY, RM, UC, UTC, WS, WTU); BONNER COUNTY, mouth of Hunt Creek, Priest Lake, *W. H. Baker 16041* (ID, WTU), 4 mi. W of Priest Lake, Lambs Creek, *W. H. Baker 16510* (ID), Priest R. at Huot's Landing, *J. H. Christ 925* (NY), Pack R. on Lake Pend Oreille, *J. H. Christ 431* (NY), Big Lightning Creek at Clark's Fork, *J. H. Christ 148* (NY), Priest R. Experimental Forest, *R. F. Daubenmire 43307* (NY, WS, WTU), *C. C. Epling 6384* (MIN, SMU, US), Lake Pend Oreille, *M. B. Dunkle in 1914* (ID), W slopes, Priest River Range, *J. B. Leiberg 2730* (ORE, US), 5 mi. W of Sand Point, *J. H. Ehlers & C. O. Erlanson 51* (MICH); BOUNDARY COUNTY, Upper Priest R., *E. Epling 7324* (MO), 19.5 mi. NNW of Sandpoint, *P. F. Stickney 1712* (ID); CASSIA COUNTY, Raft R. valley, *D. D. Biggers in 1929* (ID), Basin, *K. T. Harper 1119* (UT), 13.5 mi. S of the town of Rock Creek, *N. H. Holmgren 6175* (ARIZ, ASU, BRY, KANU, NY, US, UTC, WTU); CLEARWATER COUNTY, 10 mi. E of Boville, *A. Cronquist & Q. Jones 5983* (CAN, COLO, DAO, DS, GA, GH, ID, ILL, KANU, MICH, MT, NY, RSA, TEX, UC, US, UTC, WS, WTU), Oviat Meadows, *D. Wagner 89* (WS), Shanghai Mt., *R. L. Lingfelter 488* (DS, IDS, MT, NY, RSA, SMU, UC, WS, WTU), Clearwater National Forest, 7 mi. W of Bungalow Ranger Station, *W. H. Baker 14460* (ID, RSA); ELMORE COUNTY, Manyon Creek, *J. F. Macbride 579* (RM), Boise National Forest, Bear Creek, *F. A. MacFadden 15553* (ISC, OKLA); FREMONT COUNTY, Big Springs, *J. H. Christ 5615* (NY), Big Springs, 5 mi. E of Yellowstone Hwy, *A. Cronquist 1607* (IDS, MO, ND, UTC), Henry's Fork of Snake R., just below Big Falls, *A. Cronquist 1789* (IDS, MIN, UTC); IDAHO COUNTY, Nez Perce National Forest, above the Selway at Falls Point Lookout, *W. H. Baker 12456* (ID, RSA), near mouth of Meadow Creek, S of Selway R., *W. H. Baker 14247* (ID), Selway R. above Selway Falls, *L. Constance & R. Rollins 1664* (POM, WS), 14 mi. E of Kooskia along U.S. route 12, *G. Davidse & A. Collotzi 605* (UTC), 7.5 mi. SSE of Grangeville, *R. Daubenmire in 1959* (WS), ca. 5 mi. W of Riggins on road to 7 Devils, *C. Davidson 1607* (RSA), 2 mi. S of Pollock, *R. J. Davis 2382* (IDS, POM), Lowell, *R. J. Davis 3538* (IDS, POM), near Lowell, *C. L. Hitchcock & C. V. Muhlick 14696* (NY, WTU), 3 mi. W of Lowell, *Q. Jones 62* (DS, GH, MIN, RSA, SMU, WS, WTU), Sharp Creek, 1.5 mi. from its mouth, *J. Packard 573* (UC, WS), 5 mi. up Slate Creek from Salmon R., *J. H. Christ & W. Ward 7756* (NY); KOOTENAI COUNTY, Sandpoint Substation, Leiberg Trail, *J. H. Christ & N. Teape 3428* (NY), Cour d'Alene, *H. J. Rust 290* (ID, NY), Hayden Creek Canyon, *H. J. Rust 147* (ID), 4 July Canyon, *J. B. Leiberg 1337* (GH,

MIN, NMU, NY, ORE, POM, RM, UC, US), in the Palouse Country and about Lake Coeur d'Alene, *G. B. Aiton in 1892* (MIN, RM, WIS); Latah County, Paradise Ridge, Moscow, *W. H. Baker 1326* (ID), Moscow Mts., *L. F. Henderson in 1894* (CU, DS), Thatuna Hills, *C. Epling & Hauch 9036* (MO, US), S slope Moscow Mt., Palouse Range, *B. W. Chichester 1198* (ID), S of Helmer, *J. H. Christ & F. Gail 6908* (ID, NY), Thatuna Ridge, *R. F. Daubenmire 37446* (WS), N of Lookout, *R. F. Daubenmire 59106* (WS), E side of Moscow Mt., *X. M. Gaines 309* (WS, WTU), 5 mi. ENE of Moscow, *L. K. Henry in 1969* (CM), E Hatter Creek, *G. R. Lockard in 1961* (ID), St. Joseph National Forest, *R. Ogilvie in 1956* (DAO, UBC), Cedar Mt., *C. V. Piper 3579* (GH, WS), W slope of Bald Mt., *E. L. Richards 102* (ID); LEMHI COUNTY, Camp Tendoy, *R. J. Davis 152-35* (IDS), Salmon, *E. B. & L. B. Payson 1753* (BH, CAS, GH, H, MO, NY, RM), 12 mi. W of Salmon, *J. H. Christ 14683* (ID, WS, WTU); NEZ PERCE COUNTY, Munro's Fountain, Lake Waha, *R. K. Beattie in 1902* (WS), E of Lewiston, *J. H. Sandberg et al. 289* (DS, IA, MO, NY, ORE, POM, TEX, US), Ravine N of Lewiston, *R. F. Daubenmire in 1972* (WS), Lake Waha, *A. A. & E. G. Heller 3314* (CU, DAO, MIN, NDG, NY, UC, US, WIS); POWER COUNTY, ca. 15 mi. WSW from Pauline, Knox Canyon, *S. Welsh et al. 17372* (BRY); SHOSHONE COUNTY, mouth of Bullion Creek, *W. H. Baker 13499* (ID, RSA), N Fork St. Joe R., Avery, *Richardson in 1936* (ID), 10–12 mi. above Clarkia, along St. Maries R., *C. B. Wilson 109* (BH, GH, IDS, MO, US, WS), Clearwater Camp on Little North Fork of Clearwater R., *C. B. Wilson 462* (IDS, WS), Swamp Creek, *L. Abrams 798* (DS, NY); TETON COUNTY, S of Victor, *J. H. Christ 5298* (NY); VALLEY COUNTY, McCall, *H. Tucker 9116* (NY), Payette National Forest, W of Cascade, *J. W. Thompson 13851* (BH, CAS, DS, DUKE, GH, MICH, MO, NY, PENN, PH, POM, UC, US, WTU), Boise National Forest, head of Silver Creek, *M. Lewis 2407* (UTC); WASHINGTON COUNTY, Middle Fork Weiser R., *M. E. Jones in 1899* (POM). MONTANA: FLATHEAD COUNTY, Glacier National Park, W side of Logan Pass, *P. C. Hoch 1509* (BM, CM, E, G, K, KYO, MHA, MO, NCU, P, PE, SHIN, TUS), Blackfoot Glacier, *M. E. Jones in 1909* (POM), W side of Glacier National Park, *W. McCalla 3785* (ALTA), Lake McDonald, *L. Umbach in 1901* (WIS), *F. Vreeland 970* (CAN, MONTU, NY, US), Swan Mt. Range, *E. Chadwick 160* (MONTU), N Swan Range, Krause Creek, *J. Antos 318* (MONTU), Glacier National Park, Mt. Cannon, *L. H. Harvey 6064* (MISS, MONTU), Avalanche Camp Ground, *J. H. Thomas 11151* (DS); GALLATIN COUNTY, near Bozeman, Mt. Bridger, *J. W. Blankenship 197* (CAN, DS, H, MO, MONTU, MT, NEB, PH, POM, RM, UC, US); GLACIER COUNTY, Glacier National Park, between Lake Josephine & Lake Grinnell, *D. H. Brant 123* (WTU), woodland about Swift Current Lake, *B. Maguire 920* (UTC), 2 mi. below Gunsight Lake, *B. Maguire 921* (CU, POM, UC, UTC), 2 mi. below Grinnell Lake, *B. Maguire 922* (CU, MO, POM, UC, UTC); GRANITE COUNTY, Harrys Flat Camp, Rock Creek Canyon, *C. L. Hitchcock & C. V. Muhlick 14394* (NY, WS, WTU); LAKE COUNTY, Mission Creek, Upper Falls area, *W. P. Cottam 17233* (COLO, DAL), Flathead Lake, Yellow Bay, *Mrs. J. Clemens in 1908* (DS), *M. E. Jones 8406* (POM), *D. H. B. Ulmer, Jr. 560* (DUKE), Flathead Lake, Tepee Creek, E lakeshore, *L. R. Reynolds 192* (DUKE, MONTU, NCU), Skidoo Creek ca. 5 mi. from hwy 35, *D. Woodland 601* (DS, MONTU), Big Draw, Mill Creek Road, *L. H. Harvey 5038* (MONTU); LINCOLN COUNTY, Spar Lake, *L. H. Harvey 5473* (MONTU); MISSOULA COUNTY, above Bonner, Blackfoot Valley, *C. L. Hitchcock 1659* (CAS, MONTU, POM, RM), Missoula, *E. S. Janson in 1928* (MICH), Sapphire Mts., Plant Creek tributary of Miller Creek, *D. Ramsden 11* (MONTU), 4 mi. SW of Clinton, Lolo, W Fork Schwartz Creek, *P. F. Stickney 637* (MONTU, WTU); RAVALLI COUNTY, Bitterroot Mts., St. Regis Creek, *W. R. Sweadner in 1932* (CM), off lower St. Mary's Road, *K. H. Lakschewitz 5124* (COLO); COUNTY UNKNOWN; Prickly Pear Canyon, *R. S. Williams 650* (MIN, US), Big Belt Mts., Deep Creek Canyon, *J. W. Blankenship in 1899* (ISC, MONTU, NMU, RM), Midvale, *L. M. Umbach 668* (DS, MIN, NMU, NY, US, WIS). NEVADA: DOUGLAS COUNTY, Glenbrook, *C. F. Baker 1342* (GH, MO, NDG, NY, POM, US), 10–15 mi. SW of Carson on King's Canyon Road, *T. L. Breene 616* (ARIZ, NA, POM), 2 mi. W of Lake Tahoe junction, Kingsbury Grade, *H. L. Mason 12183* (DUKE, ID, UC), summit of Kingsbury Grade, *L. Mills & K. Beach 1252* (NA), Daggett's Pass, *A. M. Ottley 995* (CU), Glenbrook on Lake Tahoe, *I. Tidestrom 10318* (US); ELKO COUNTY, Humboldt Forest, Lime Creek, *B. Crane in 1937* (UTC), right fork of Lamoille Canyon, *L. L. Loope 1050* (DUKE), 2.5 mi. above town of Jarbridge, *P. Train 806* (DAO, DS, MO, NA, NY, POM); ORMSBY COUNTY, Lake Tahoe, *K. H. Beach 230* (KSC), Carson City, Carson Range, *A. Pinzl 951* (NY); WASHOE COUNTY, Lake Tahoe, Creek at Incline, *W. A. Archer 6701* (ARIZ, DS, MICH, MO, NA, NY, POM), 25 mi. SW of Reno, *W. A. Archer 5884* (DAO, NA, POM, UC), vicinity of Reno, *A. Hitchcock 485* (US), Hunter Creek Canyon, *P. B. Kennedy in 1912* (DS), near Franktown, Lewer's Ranch, *P. Lehenbauer in 1929* (NA), W side of Little Valley, *H. Mozingo in 1971* (NLU). NEW MEXICO: CATRON COUNTY, ca. 10 air mi. ESE of Mogollon in Gila Wilderness, *R. Spellenberg et al. 4505* (NY); LINCOLN COUNTY, White Mts., vicinity of Rio Bonito, W of Bonito Lake, *B. Hutchins 3490* (UNM); OTERO COUNTY, White Mts., Mescalero Reservation, Ruidosa Creek, *L. C. Hinckley 720* (ARIZ, GH, NY, TEX). OREGON: BAKER COUNTY, Kettle Creek Camp, *G. Mason 6296* (ORE, OSC), near Head's Cabin, *S. C. Head 1075* (OSC, RSA), Blue Mts., Anthony Creek, *H. Ripley & R. Barneby 9476* (RSA); BENTON COUNTY, Corvallis, *H. C. Gilbert 30* (OSC), Philomath, *M. Stason*

in 1925 (UC), near Philomath, *C. Gregg in 1956* (RSA), Kings Valley, *B. Miller 104* (OSC), upper Greasy Creek, *E. Hansen in 1939* (DS), Boy Scout Camp at foot of Alsea Mt., *Mrs. J. Smith in 1960* (OSC, PENN); CLACKAMAS COUNTY, Mt. Hood, Alder Creek, *J. W. McFarland in 1941* (BH), Rhododendron, *D. Overlander in 1945* (KANU, OSC, TEX, WS), Milwaukie, *W. N. Suksdorf in 1893* (WS); COOS COUNTY, 2 mi. above Broadbent, *L. Henderson 10153* (ORE), Arago, *T. Lammi in 1939* (OSC), Coos Bay, head of Coos River, *H. D. House 4833* (US); CROOK COUNTY, Ochoco Mts., between Pineville & Mitchell, *A. Cronquist 7374* (NY, WS), Ochoco National Forest, upper Scisson Creek, *M. Kucera 206* (WS), Blue Mt. between Mitchell & Pineville, *H. Mason 3572* (UC); CURRY COUNTY, near Lowery's, 16 mi. below Agness, *L. Henderson 11703* (ORE), 4 mi. N of Port Orford, *M. Peck 8592* (BH, GH, MO, NY), ca. 12 mi. from Powers, *L. Leach 2428* (ORE); DESCHUTES COUNTY, Four-mile Spring, *L. Detling 5789* (ORE), Deschutes National Forest, Sister's Ranger Station, *R. Ferris & R. Duthie 587* (DS); DOUGLAS COUNTY, 0.5 mi. S of Glide, *E. Earle 4908* (NY, PENN), ca. 20 mi. W of Crater Lake, SE of Elephant Head, *R. Mitchell 222* (OSC), Cow Creek, 1 mi. below Nichols Station, *L. Ward 57* (US); Grant County, 12 mi. S of Dayville, *A. Cronquist 7610* (NY, RSA, WS, WTU), Blue Mts., near Dixie Station, *L. Henderson 5633* (CAS, DS, MO, ORE), 21 mi. E of Seneca, Lake Creek Guard Station, *A. N. Steward 6951* (CAS, DAO, GH, ISC, OSC, UBC, WTU), John Day R. near mouth of Widow Creek, *M. E. Peck 10148* (DS, POM); HARNEY COUNTY, Emigrant Creek, *M. E. Peck 3748* (WILLU), Blue Mts., Sawtooth Creek, *L. F. Henderson 8884* (CAS, ORE), 12.5 mi. E & 9.75 mi. due S of Frenchglen, *C. G. Hansen 841* (OSC); HARNEY-GRANT COUNTIES, Lonesome Creek Area, Malheur National Forest, *D. B. Pingley in 1961* (WVA); HOOD RIVER COUNTY, Mt. Hood, S slope, *L. Benson 2524* (DS, MO, NY, POM, US), Mt. Hood National Forest, Tilly Jane Creek, *Evinger & Goodding 653* (OSC), Dry Creek Falls, Cascade Locks, *T. Gustafson 78* (OSC), Locks, *L. F. Henderson 831* (MO), Eagle Creek near Bonneville, *N. W. Rickett 1608* (UMO); JACKSON COUNTY, Wimer, *E. Hammond in 1892* (CM, RM, US), Grizzly Peak, NE of Ashland, *H. Mason 4069* (UC), Sykes Creek, *E. Hammond 150* (ISC, MO), Miller Lake Trail, *H. M. Gilkey in 1940* (OSC), Johnson Prairie along Jenny Creek, *E. I. Applegate 5207* (DS), along Beaver Creek, *F. Hoffman 2550* (UC); Jefferson-Deschutes County line, Black Butte, NW of Sisters, *J. M. & M. Johnson 483* (DS, OSC, US); JOSEPHINE COUNTY, W Fork of Williams Creek below Cave Camp, *E. I. Applegate 8712* (DS), Deer Creek Valley, *H. L. Dale in 1919* (DS), Oregon Caves to Mt. Elijah, *L. Detling 6478* (ORE), T40S, R5W, Sec. 21, *R. Waring 756* (OSC), Oregon Caves National Monument, Big Meadow, *E. I. Applegate 10551* (DS), Williams Creek Trail near Oregon Caverns, *R. Beattie 5612* (US), Siskiyou Mts., Grayback Creek, *R. H. Whittaker SS93* (WS), Dwight Creek on Redwood Hwy, *D. K. Kildale & J. W. Gillespie 8141* (DS); KLAMATH COUNTY, Nelson Creek, N end of Swan Lake valley, *E. I. Applegate 4406* (DS, WILLU), Crater Lake National Park, Redblanket Canyon, *W. H. Baker 7074* (ID, NY, RSA, WS), Crater National Forest, branch of Cherry Creek, *J. Rose 1066* (MO), Crater Lake National Park, bottom of Anna Creek Canyon, *E. I. Applegate 10902* (DS, WS), W side of Klamath Lake, mouth of Cherry Creek, *F. Coville & E. I. Applegate 300* (US); LAKE COUNTY, 8 mi. S of Lakeview, *M. E. Peck 14338* (WILLU); LANE COUNTY, 2 mi. W of Coburg, *W. H. Baker 884* (ID, OSC), Fairview Mt., W slope, *W. H. Baker 1029* (ID, OSC), woods of Spencer Butte, *R. Brown 107* (ORE), E of Eugene, Camp Creek, *L. Constance in 1928* (UC), Swiss Home, *L. Detling 2884* (ORE, UC), River Camp Forest Campground, N Fork Willamette R., *O. Ireland 1521* (ORE), 15 mi. SW of Junction City, *G. Mason 10233* (ORE), Horse Creek, *M. Gorman 1656* (US); LINCOLN COUNTY, 2 mi. W of Harland, *L. J. Dennis 2722* (NCU, NLU, OSC, TUR, UMO, UTC); LINN COUNTY, SW base of Mt. Jefferson, Parmelia, *M. E. Peck 9230* (MO, WILLU), Crabtree, *D. W. Hatch 21* (OSC), Santiam R., *H. M. Gilkey in 1934* (OSC), near Fish Lake, *E. I. Applegate & F. Coville 618* (DS, ND, US), N side Peterson Butte, *L. Whitaker in 1938* (OSC), W of Corvallis on Mary's Peak, *H. Gilbert 30* (US); MARION COUNTY, Gates, *M. Gorman 4102* (PH, WS), Detroit, *M. Gorman 4108* (DS, PH, TEX, WS), Salem, *M. E. Peck 3750, 3751* (WILLU), Silverton, *J. C. Nelson 157* (DS), 0.5 mi. E of Orville, *J. C. Nelson 3760* (PH); MULTNOMAH COUNTY, Portland, *A. Kellogg & W. Harford 989* (US), *F. Kelsey in 1888* (NY), *G. H. Hicks 206* (MIN), *L. F. Henderson 363* (OSC), Sauvie's Island, *T. Howell in 1881* (MIN, OSC), Columbia Gorge E of Crown Point, *L. Detling 7108* (DS, ORE), hills of W Portland, *J. W. Thompson 235* (DS, WTU), banks of Columbia R. below Oregon, *J. Donaldson in 1946* (OSC), Mt. Scott, *E. P. Sheldon S12282* (DS, ORE, TEX); TILLAMOOK COUNTY, N Fork Wilson R. a few mi. downstream from Blue Lake, *K. L. Chambers 4101* (OSC), Miami River, *G. E. Merrill 201* (ND, WTU); UMATILLA COUNTY, 5 mi. W of Meacham, *M. E. Peck 3749* (WILLU); UNION COUNTY, ca. 3 mi. E of Cove, *G. Mason 2436* (ASU), ca. 2.5 mi. N of Boulder Park, *G. Mason 5446* (ORE); WALLOWA COUNTY, S of Enterprise, *D. Cole 182A* (ORE), near BC Creek at Wallowa Lake, *G. Mason 5227A* (OSC, RSA), 2 mi. from Power House Road on Lake Basin Trail, *G. Mason 5835* (ORE), ca. 2 mi. S of Joseph, *G. Mason 7903* (ASU), Horse Creek Canyon, *E. Sheldon 8145* (GH, MO, NY, RM, WTU), Downey's Gulch, *E. Sheldon 8322* (NY); WASHINGTON COUNTY, Forest Grove, *J. W. Thompson 867* (DS, WTU), Scroggin's Valley, *J. W. Thompson 4297* (DS, MO, OKLA); WHEELER COUNTY, Widow's Creek, *M. E. Peck 10148* (WILLU), Ochoco National Forest, *S. Warg in 1933* (OSC). UTAH: BOXELDER COUNTY, Raft River Mts., George

Creek Canyon, *S. J. Preece, Jr. 815* (RSA, UT), Perry Canyon, *W. P. Cottam et al. 16228* (UT); CACHE COUNTY, Wellsville Mts., near the top of Schaefer Canyon, *P. Camp in 1967* (UTC), Wellsville Canyon, *W. S. Flowers 1711* (UT), Logan Canyon, *B. Maguire 13868* (BRY, DAO, UTC, WTU), *13869* (BRY, WTU); DAVIS COUNTY, Wasatch Mts., Mueller's Park, *J. L. Moore 100* (LTU, UT); JUAB COUNTY, Mt. Nebo, at Loop Spring, *F. Peabody 790* (BRY); MORGAN COUNTY, Wasatch Mts., Peterson Canyon, *Pammel & Blackwood 3797* (ISC, MO); SALT LAKE COUNTY, Wasatch Mts., Alta, *M. E. Jones 1276* (CM, GH, MICH, NY, POM, US), near Salt Lake City, City Creek Canyon, *M. E. Jones in 1880* (POM), *F. E. Leonard in 1883* (ISC, NY), Silver Lake, American Fork Canyon, *M. E. Jones in 1895* (ORE, RM), E of Salt Lake City, Red Butte Canyon, *L. Arnow 1834* (NLU, RSA, UT), *2219* (BRY, UT, UTC), *J. Clemens in 1909* (MO), Moss Falls, Big Cottonwood, *W. P. Cottam 8353* (UT), *B. Harrison 9443* (BRY), Emigration Canyon, *C. Smith 1854* (RM, UTC), Neffs Canyon, *S. Winburn in 1971* (UT); UTAH COUNTY, Mt. Timpanogos, Bear Canyon, *K. Allard 451* (BRY), Mt. Timp, *W. P. Cottam 1235* (BRY), Provo, *M. Tracy s.n.* (COLO), Wasatch Range, Big Tree Campground, *W. P. Cottam et al. 15095* (ARIZ, DS, RSA, UC, UT, WTU), Aspen Grove, *S. Flowers 148* (UT), Provo Canyon, Bridal Veil Falls, *S. L. Welsh 3229* (BRY, ISC); WEBER COUNTY, N Fork Ogden R., trail to Ben Lomond, *S. Clark 2098* (BRY), Ogden, *G. W. Letterman in 1885* (MIN), N of Snow Basin Road, Wheeler Creek, *S. Clark 2177* (BRY). WASHINGTON: ASOTIN COUNTY, Cottonwood Creek SW of Anatone, *A. Cronquist & Q. Jones 5940* (CAN, COLO, DAO, DS, DUKE, GA, ID, ILL, KANU, MICH, MIN, MT, NCSC, NY, RSA, SMU, TEX, UC, US, UTC, WS, WTU, WVA); CHELAN COUNTY, Entiat Valley, Silver Creek, *G. E. Merrill 259* (WTU), Horseshoe Basin, *H. St. John & L. Ridout 3578* (MT, WS), Wenatchee National Forest, valley of White R., *H. St. John 4794* (WS), Bridge Creek near Chelan Lake, *M. E. Jones in 1911* (DS, POM), Chelan Lake, Stehekin, *M. E. Jones in 1911* (POM); CLALLAM COUNTY, Lake Crescent, *H. & S. Parks 0669* (UC), Olympic Mts., *A. D. E. Elmer 2564* (DS, MIN, MO, NY, ORE, POM, SMU, US, WS), Port Crescent, *W. H. Lawrence 246* (MO, NA, WS), Olympic National Park, 8.6 mi. S of the entrance to Heart of the Hills, *R. Riggins 763* (ISC), Mt. Angeles, *E. B. Webster 46* (NDA), Hurricane Ridge, *E. B. Webster 1238* (WTU), Olympic Mts., along Elwah R., vicinity of Altaire Public Camp, *I. L. Wiggins 9416* (DS, GH, NY, RM); CLARK COUNTY, Lacamas Creek, *C. English, Jr. 462* (BH, US); COLUMBIA COUNTY, Wenaha Forest Reserve, Blue Mts., Tallow Flat, *N. T. Darlington 137* (WS), along Tukanon R., *Lake & Hull 533* (NY); FERRY COUNTY, 15 mi. W of Kettle Falls, Sherman Creek, *L. Boner & V. Weldert 238* (CAS, DS, GH, MIN, NY, RM, UTC, WS, WTU), Barnaby Creek at its confluence with the Columbia R., *H. T. Rogers 567* (GH, MO, NY, POM, UC, WS, WTU); GARFIELD COUNTY, Tucannon R. T8N, R42E, Sec. 7, *M. Barkworth 440* (WS); GRAYS HARBOR COUNTY, Stevens Creek, *G. N. Jones 3947* (DS, POM, WTU), Hoquiam, *F. H. Lamb 1136* (MO), Montesano, *J. M. Grant in 1918* (GH, MO), vicinity of Quinault Ranger Station, *A. Lasseigne in 1973* (ISC); ISLAND COUNTY, Camano Island, *N. Gardner in 1895* (UC), Whidbey Island, Deception Pass Park, *H. W. Smith 1054* (WS); JEFFERSON COUNTY, Hoh R., *I. C. Otis 1289* (WS), head of Big Quilcene R., *J. W. Thompson 7929* (GH, MO, NO, PH, UC, WTU), S side of Olympic National Park, Quinault Rain Forest, *T. G. Yuncker & W. H. Welch 18893* (NCU, UC), Quinault R. between Enchanted Valley & 3 mi. S of O'Neil Creek Shelter, *G. B. & R. P. Rossbach 470* (CAS, DS, RM, WTU), Hoh R., near Jackson Guard Station, *J. E. Schwartz 11A* (WTU), Seattle, *L. Benson 1486* (DS, POM), *A. Eastwood 9603* (CAS), *S. M. Zeller in 1910* (MIN, MO), above Embro, *I. C. Otis 739* (CAS, WS), Lake Washington, *T. E. Savage et al. in 1898* (IA, MIN), E side of Lake Washington, *J. H. Thomas 5744* (DS), S Seattle, *J. W. Thompson 5179* (DS, MIN, WTU); KITSAP COUNTY, 12 mi. W of Bremerton, *W. J. Eyerdam 1647* (DAO, ID, WS, WTU), Seabeck, *L. A. Dillon 484* (OSC, WS); KITTITAS COUNTY, Mt. Stuart, *A. D. E. Elmer 1187* (MIN, US); KLICKITAT COUNTY, Bingen Mts., Bingen, *W. N. Suksdorf 5667* (WS), Klickitat R., *W. N. Suksdorf in 1886* (WS), Trout Lake, *W. N. Suksdorf in 1882* (WS), near spring in woods, *W. N. Suksdorf in 1885* (BH, CAN, MO, US, WS), Falcon Valley, *W. N. Suksdorf 379* (WS); LEWIS COUNTY, Hogman, *F. Lamb 1136* (NY, PH), clearing near Cripus R., *Mrs. M. E. Jones in 1941* (DS); MASON COUNTY, Skokomish Valley, *T. Kincaid in 1892* (WS), Lilliwap Falls on W side of Hood Canal, *F. Meyer 507* (MO, WTU), near Wagonwheel Lake above Staircase Lodge, *P. A. Munz 11491* (CAS, DS, UC, WS); OKANOGAN COUNTY, Okanogan Forest, *W. W. Eggleston 13526* (US), 1 mi. N of Conconully, *A. N. Steward in 1919* (OSC), near Conconully, near summit of Muckamuck Lookout, *R. Bigelow 132* (DS, GH, MO, WTU), Granite Mountain Trail, Twin Firs Camp, *C. B. Fiker 292* (WS), Eight Mile Creek, Methow R., *J. W. Hungate in 1955* (WS), Republic, Sweat Creek, *J. W. Hungate 34* (WS), Wenatchee Valley, Peshastin, *J. Sandberg & J. Leiberg 506* (BH, CAS, GH, ILL, MO, NY, ORE, POM, UC, US, WS), Chelan National Forest, valley of War Creek, *H. St. John et al. 3707* (WS); Pacific County, 2 mi. SW of Raymond, *D. Hedrick & F. Clifton 142* (ALTA, CM, MO, POM, WS); PEND OREILLE COUNTY, Sec. 34, T39N, Sullivan Creek, *E. F. Layser 232* (WS); PIERCE COUNTY, Mt. Ranier National Park, Hansen Camp, *L. R. Abrams 9220* (DS, MO, POM, RM), Mt. Ranier, Longmire, *A. Lindsay 4587* (NA, UTC), Mt. Ranier, Nisqually Glacier, *H. Cowles 801* (MO), Ft. Lewis, *D. Keil 2159-c* (ASU), White River to Summerland, *P. H. Raven 8695* (CAS), La Grande, *K. M. Wiegand 1745* (CU), Sumner, Elhi Hill,

C. Grainger in 1910 (WTU); SAN JUAN COUNTY, San Juan Islands, Mt. Constitution, *S. M. & E. B. Zeller 906* (MIN, MO, NY), Friday Harbor, *S. M. & E. B. Zeller 905* (CM, GH), Trout Lake, *M. E. Peck 13072* (WS); SKAGIT COUNTY, Pleasant Ridge, *H. Mason 3809* (POM, UC); SKAMANIA COUNTY, Columbia National Forest, Panther Creek Road below bridge, *W. Bullard 5832* (NA), Cape Horn, *W. N. Suksdorf in 1894* (WS); SNOHOMISH COUNTY, Mt. Dickerman, *J. W. Thompson 8805* (DS, MIN, NY, US, WTU), 10 mi. N of Seattle, *W. Eyerdam in 1931* (UC), N slope of Mt. Pilchuck, *J. W. Thompson in 1952* (RM, UT), Cascade Mts., Big Four Inn, *J. W. Thompson 14701* (ALTA, COLO, DS, GH, MICH, MO, NY, OKLA, RSA, UBC, UC, W, WTU), Marysville, *J. M. Grant in 1930* (KYO, UC), Edmonds, *G. Hoppe in 1934* (SMU), Silverton, *Mrs. L. A. Rouck 76* (WS), ca. 2 mi. SSE of Verlot, *G. Douglas 527* (ALTA), Perry Creek Trail on S Fork Stillaquamish R., *L. K. Henry in 1969* (CM), Snoqualmie National Forest, *E. Purer 7718* (MO); Spokane County, Hangman Creek, *W. N. Suksdorf in 1889* (WS), Mt. Spokane ("Mt Carleton"), *F. O. Kreager 201* (GH, MIN, MT, NY, UC, US, UTC, WS, WTU), Mt. Kit Carson, *R. Sprague 691* (WS), canyon above Bonnie Lake, *H. St. John et al. 3291* (WS), E of Spokane, NE end of Spokane Lake, *O. E. & G. K. Jennings 8626* (CM); STEVENS COUNTY, 10 mi. W of Chewelah, *R. Sprague 692* (WS), heart of Huckleberry Mts., Chamakane R., *T. Large 3* (WS); THURSTON COUNTY, ca. 5 mi. W of Olympia, *F. Meyer 1581* (BH, GH, ISC, MIN, MO, NCSC, UC, UTC, WIS), Olympia, *E. C. Townsend in 1904* (MO, UC, WS); WAHKIAKUM COUNTY, Alochaman R., *H. St. John 8764* (WS); WALLA WALLA COUNTY, Waitsburg, *R. Horner R110* (GH), 2 mi. S of Walla Walla, *Hitchcock & Muhlick 8281* (BH, CAN, CAS, DS, GH, IDS, ISC, MO, NY, PH, RM, TRT, UC, UTC, WS, WTU), Blue Mts., *C. Piper 2409* (POM, WS); WHATCOM COUNTY, Mt. Hermann, *J. W. Thompson 5691* (DS, GH, MIN, WTU), Mt. Baker National Forest, Goodell Creek, *W. C. Muenscher 9953* (CU), Northwood, *W. C. Muenscher 5057* (CU, GH, MO), Northwood Swamp, *W. C. Muenscher 8269* (CU, UC, US), Forest Grove, *W. C. & M. W. Muenscher 5474* (BH, CU), Mt. Baker region, Bagley Lake, *J. W. Thompson 5377* (DS, WTU), Bellingham, *E. Hardin 898* (WS), Gooseberry Point, *W. C. & M. W. Muenscher 5981* (CU, MIN), Twin Lakes, Winchester Mt., *H. St. John 9032* (WS), Fairhaven, *W. N. Suksdorf* (WS), Mt. Baker National Forest, Glacier Creek, *W. C. Muenscher 8268* (CU, PH), Goshen, *W. C. & M. W. Muenscher 5475* (BH, CU, GH); YAKIMA COUNTY, Mt. Adams, Seggenbach, *W. N. Suksdorf 8288* (BH, WS), Yakima region, *T. Brandegee 502* (MO). WYOMING: CARBON COUNTY, Ferris Mts., *E. Nelson 4955* (CM, CU, NY, POM, RM, US); CROOK COUNTY, ca. 10 mi. N of Sundance, Bear Lodge Range, *C. L. & M. W. Porter 9099* (DS, MIN, RM, SASK, TEX, UC, WIS, WTU); NATRONA COUNTY, Casper Mt. area, Garden Creek Falls, *F. X. Jozwik 174* (RM, SASK); PARK COUNTY, Yellowstone National Park, SW shore of Flat Mt. Arm of Yellowstone Lake, *L. Anderson 1233* (UTC); SHERIDEN COUNTY, Lions Den, *V. Willets 259* (RM); TETON COUNTY, Targhee National Forest, S Teton Canyon near Devil's Staircase, *L. Anderson 602* (CAS, GH, OSC, RM, UC, UTC, WS, WTU), Grand Teton National Park, near junction of Death Canyon & Phelps Lake, *R. J. & R. W. Shaw 1597* (UTC), Death Canyon, *H. V. Truman 54392* (RM), summit of Teton Pass, *E. D. Merrill & E. N. Wilcox 1180* (GH, RM, US), Teton Mts., *A. & E. Nelson 6493* (BRY, CM, CU, DS, GH, ILL, ISC, KSC, MIN, MO, NEB, NMU, POM, RM, US).

Circaea alpina subsp. *pacifica* is recognized by having subentire leaves with usually rounded bases, a firm stem bearing at least a few recurved hairs (at least on the upper internode or in the nodal areas) and glandular pubescent raceme axes. Large plants closely resemble *C. lutetiana* in habit and several specimens from the Rocky Mountains have been misidentified as that species. However, in position and size of the flowers and in the fruits *C. alpina* subsp. *pacifica* is unmistakable. The flowers are held on erect or ascending pedicels and open before elongation of the raceme axis as in *C. alpina* subspp. *alpina*, *imaicola*, and *micrantha*.

In some ways the situation in *C. alpina* subspp. *pacifica* and *caulescens* is homologous to that found in other groups of plants disjunct between western North America and eastern Asia. These two subspecies have relatively thick pubescent stems and are more robust than *C. alpina* subsp. *alpina*, with which they both come in contact, but the differences in the position of flowers at anthesis, pubescence of the raceme axis, and texture and toothing of the leaves tend to rule out the possibility that one was derived from the other. It seems more likely that *C. alpina* subspp. *caulescens* and *pacifica* may represent an example of convergent evolution in similar but widely separated habitats.

Two characters that have been used in the past to separate *C. alpina* subsp. *pacifica* from subsp. *alpina* have proved to be nearly useless. Reddened nodes, while not common in *C. alpina* subsp. *pacifica* do occur in that entity and, although many plants of subsp. *alpina* do have reddened nodes, a large majority do not. Those plants of *C. alpina* subsp. *alpina* that do have reddened nodes are usually from more exposed habitats, woodland plants being entirely green. The absence of minute bracteoles have been used as a diagnostic character for recognizing *C. alpina* subsp. *pacifica* since Ascherson and Magnus (1871) first described the plants. This character is unreliable, many plants having bracteoles beneath at least a few of the pedicels of a raceme.

7e. **Circaea alpina** L. subsp. **alpina.**—FIG. 24.

Circaea minima L., Mant. 2: 316. 1771. As stated by H. E. Richter, Syst. Veg. 2: 25, Index, p. 47. 1835, this is undoubtedly an error for *C. alpina* L.
Circaea minima Lam., Fl. Fr. 3: 473. 1778. Nom. subs. *C. alpina* L. in syn.
Circaea decumbens Gilib., Fl. Lituan. 2: 127. 1782.
Circaea alpina L. var. *intermedia* Willd., Sp. Pl. 1: 54. 1797. TYPE: At base of mountains in the cold part of Europe.
Circaea racemosa Hull, Br. Fl. 6. 1799. Pro parte nom. subs., *C. alpina* L. and *C. lutetiana* L. in syn.
Circaea racemosa Hull var. *alpina* (L.) Hull, Br. Fl. 7. 1799.
Circaea alpina L. α *minor* Schrad., Fl. Germ. 1: 204. 1806.
Circaea cordifolia Stokes, Bot. Mat. Med. 1: 26. 1812. Nom. subs., *C. alpina* L. in syn.
Circaea alpina L. forma *composita* Lasch, Linnaea 2: 446. 1827. TYPE: E. Germany, Neumark.
Circaea alpina L. forma *ramosa* Lasch, Linnaea 2: 446. 1827. TYPE: E. Germany, Neumark.
Circaea alpina L. forma *simplicissima* Lasch, Linnaea 2: 446. 1827. TYPE: E. Germany, Neumark.
Circaea lutetiana L. var. *alpina* (L.) Torr., Rep. Bot. Dept. Surv. N.Y. Assembly 50: 136. 1841.
Circaea alpina L. α *fertilis* Döll, Rheinische Fl. 746. 1843.
Ocimastrum minimum Rupr., Fl. Ingr. 367. 1860. Nom. subs., *C. alpina* L. in syn.
Circaea lutetiana L. var. *alpestris* Schur, Enum. Pl. Transs. 214. 1866. TYPE: In moss hummocks in the fir region of the Arpas, 5,000 ft, July.
Regmus alpinus (L.) Dulac, Fl. Hautes Pyr. 328. 1867. Nom. illegit.
Circaea lutetiana L. subsp. *alpina* (L.) H. Lév., Monde des Pl. 7: 71. 1898.
Carlostephania minor Bubani, Fl. Pyrenaea 2: 660. 1900. Nom. illegit.
Circaea lutetiana L. race *alpina* (L.) H. Lév., Bull. Acad. Int. Geogr. Bot. 22: 220. 1912.
Circcaea pacifica Asch. & Magnus forma *dentata* H. Lév., Bull. Acad. Int. Geogr. Bot. 22: 222. 1912. "Idaho, Utah, Colorado." No specimens cited.
Circaea alpina L. var. *aleutica* Nieuwl., Amer. Midland Naturalist 3: 184. 1914. TYPE: United States, Alaska, Spacious Bay, 16 July 1895, *M. W. Gorman 199* (US, holotype; NY, isotype).
Circaea caulescens (Komarov) Nakai ex Hara var. *rosulata* Hara, J. Jap. Bot. 10: 591. 1934. TYPE: U.S.S.R., Sakhalin, Tonnai-cho, August 1906, *G. Nakahara* (TI, holotype).
Circaea caulescens (Komarov) Nakai ex Hara var. *glabra* Hara, J. Jap. Bot. 10: 590. 1934. TYPE: Japan, Honshu, Prefecture Nagano (Prov. Shinano), Mt. Yatsuga-dake, 19 August 1902, *Y. Yabe* (TI, holotype).
Circaea caulescens (Komarov) Nakai ex Hara forma *ramosissima* Hara, J. Jap. Bot. 10: 591. 1934. TYPE: Japan, Shikoku, Prefecture Ehime (Prov. Iyo), Mt. Ishidzuchi, 9 August 1898, *R. Yatabe*? (TI, holotype).

Plants (0.3–)0.5–2.5(–3) dm tall, totally glabrous except for minute cilia along the leaf margin, sometimes on the petiole and sometimes also with soft, short glandular hairs on the axis of the inflorescence. The stem and petioles soft and somewhat succulent, terete, flattened in pressing and then appearing winged. Stem green or occasionally the nodes purple, rarely the entire stem purple in plants of exposed habitats. Leaves pale green, translucent; those near the summit of the stem the largest, 1.5–5.5(–7.5) cm long, 1.5–4.5(–5.5) cm wide, very abruptly reduced in size upward to the base of the inflorescence and then bractlike,

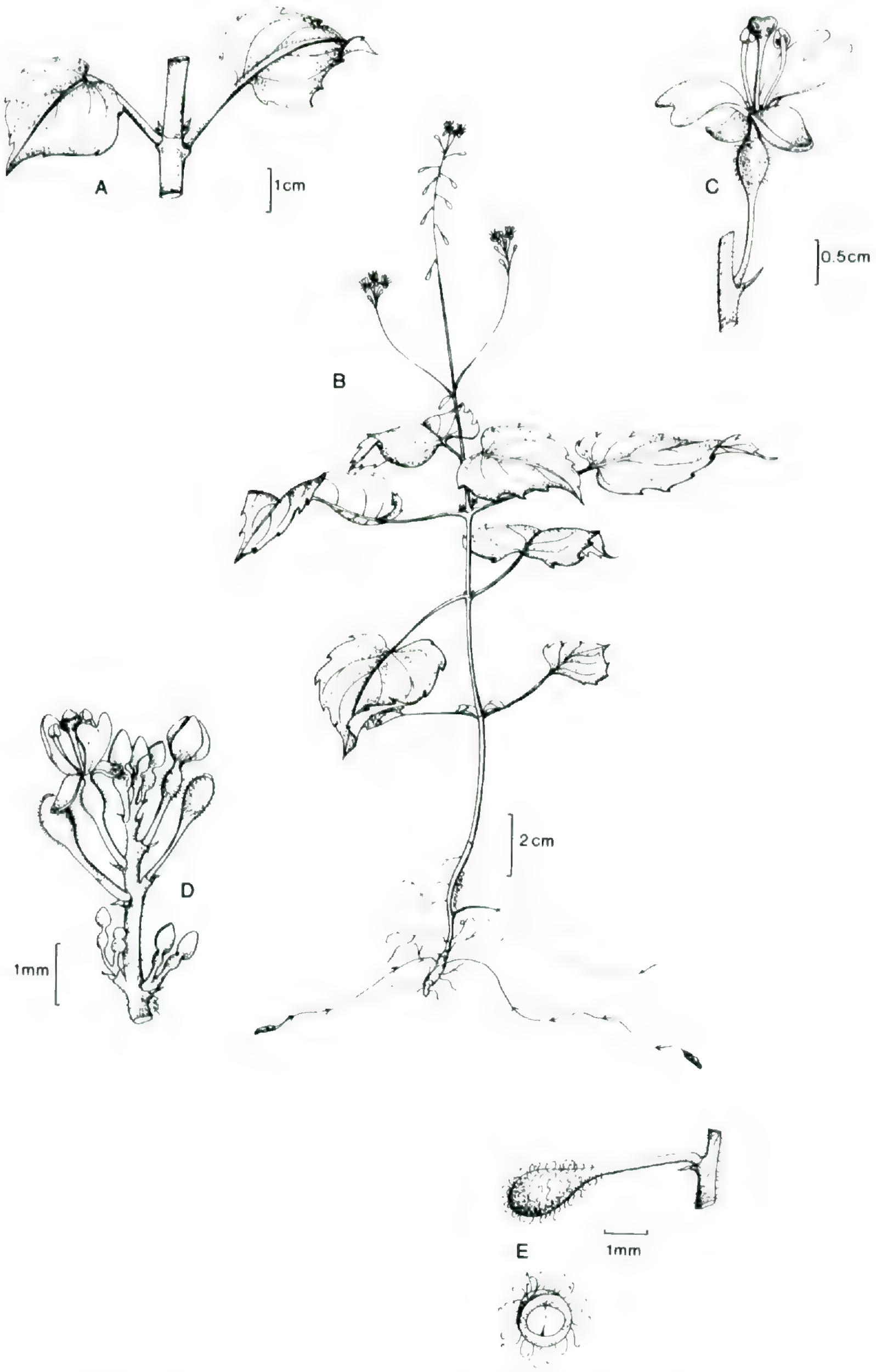


FIGURE 24. *Circaea alpina* L. subsp. *alpina*.—A. Node of upper stem.—B. Habit.—C. Flower.—D. Young inflorescence.—E. Fruit. From *Boufford 18803* (KYO, MO).

gradually to abruptly reduced downward, sometimes clustered near the summit of the stem and then appearing somewhat whorled. Leaves ovate to very broadly so, rarely almost circular in outline, short acuminate to acute at the apex, cordate to subcordate, less commonly truncate or rounded at the base, conspicuously dentate, glabrous except for falcate cilia, 0.1–0.2 mm long along the margins, rarely with a few short soft, falcate cilia ca. 0.1 mm long on the upper surface

near the petiole. Petiole 0.3–3(–4) cm long, semi-terete in life, flattened and appearing winged in herbarium specimens; glabrous or sparsely pubescent in lines along the upper surface with short, upwardly curved, falcate hairs 0.1–0.2 mm long; with, or occasionally without, reduced branches arising in the axils. Inflorescence glabrous to densely pubescent with short, capitate and clavate-tipped glandular hairs 0.1–0.2 mm long; terminal on the main stem and upper axillary branches, or, in plants of exposed habitats, at the tips of axillary branches arising from near the base of the stem. The inflorescence simple or more commonly, with alternate or opposite lateral racemes from the base, these subtended by reduced leaves or leaflike bracts. Flowering pedicels glabrous, 0.7–2.4 mm long, ascending or erect; the flowers opening before elongation of the raceme and clustered at the apex; with a setaceous bracteole, 0.1–0.4(–0.6) mm long, at the base. Fruiting pedicels 1.5–3.8(–4.5) mm long. Buds glabrous; from the summit of the ovary, 0.8–2.2(–2.5) mm long, 0.4–0.9(–1.3) mm thick, white, occasionally pink or purple at the apex or sometimes the buds entirely pink. Ovary 0.5–1.5 mm long, 0.3–0.6 mm thick at anthesis, clavate to narrowly so; pubescent, with soft, short, translucent, uncinate hairs. Floral tube represented by a mere constriction to 0.5 mm long, 0.1–0.2 mm thick at the narrowest point, funnelform. Sepals 0.9–1.8(–2.2) mm long, 0.6–1.2 mm wide, white or pink, occasionally tinged with purple at the apex; oblong to ovate, sometimes broadly so, rounded to the obtuse or minutely mammiform apex. Petals 0.6–1.5(–1.9) mm long, 0.8–1.7 mm wide, most commonly longer than wide, white, obtriangular to obovate in outline; the apical notch 0.3–0.5(–0.7) mm deep, ¼–½ the length of the petal; the petal lobes rounded. Filaments 0.7–2 mm long; anthers 0.2–0.4 mm long, 0.2–0.3 mm thick. Style 1.1–2.1 mm long; stigma 0.1–0.3 mm tall, 0.15–0.5 mm thick. Mature fruit clavate, 2–2.5 mm long, 0.7–1.2 mm thick, the translucent, uncinate hairs 0.2–0.4 mm long. Combined length of pedicel and mature fruit, (3.7–)4.3–6(–6.5) mm long. Gametic chromosome number, $n = 11$.

TYPE: Sheet 25-2 (LINN) "*alpina*" can be taken as the lectotype. The species is common in Sweden and Linnaeus doubtless knew it well.

Distribution (Figs. 25, 26): Moist to wet places and on moss-covered rocks and logs. Circumpolar in cool temperate and boreal forests between 30° and 65° N. Lat. but restricted to high elevations at lower latitudes. From near sea level to 2,500 m. Flowers, June to August, rarely into early September.

Representative specimens examined:

NORTH AMERICA

CANADA. ALBERTA: Marten Mt., E of Lesser Slave Lake, *L. Abele & W. Peterson 165* (ALTA); T75, R15, W4, 6 mi. E of junction May Tower Road & McMurry Hwy, *P. Achuff 1024* (ALTA); T84, R11, W4, mile 127 of McMurry Hwy, *P. Achuff 1026* (ALTA); ca. 100 mi. NW of Edmonton, 15 mi. SW of Swan Hills, *P. Achuff 1615* (ALTA); Jasper, Edson Dist., W of Lake Iosegun, *B. Boivin & J. Perron 12541* (DAO, GH, NY, SASK); Slave Lake Dist., near Assineau R., *A. Brinkman 4360* (CU, NY): Jasper, *H. H. Brown in 1933* (TRT); Bicke Lake, Big Island, *W. Cody & R. Gutteridge 7068* (ALTA, DAO, GH); SW end of Lake Athabasca, 10 km S of Mamawi Lake, *D. Dobbs & W. Frieson 328* (SASK); 25 mi. N of Swan Hills, *M. G. Dumais et al. 43* (ALTA); Hutch Lake, N of High Level, *M. G. Dumais et al. 94* (ALTA, DAO); NW of Edmonton on hwy 43, ca. 45 mi. W of Whitecourt, *M. G. Dumais et al. 327* (ALTA); SW end of Long Lake, in Provincial Park, *M. G. Dumais & C. Watson 1702* (ALTA, CAN, DAO); 85 mi. NE of Slave Lake, Wabasca on S tip of N Wabasca Lake, *M. G. Dumais & K. Anderson 3292* (ALTA); S shore of Cold Lake, French Bay on the Alberta-

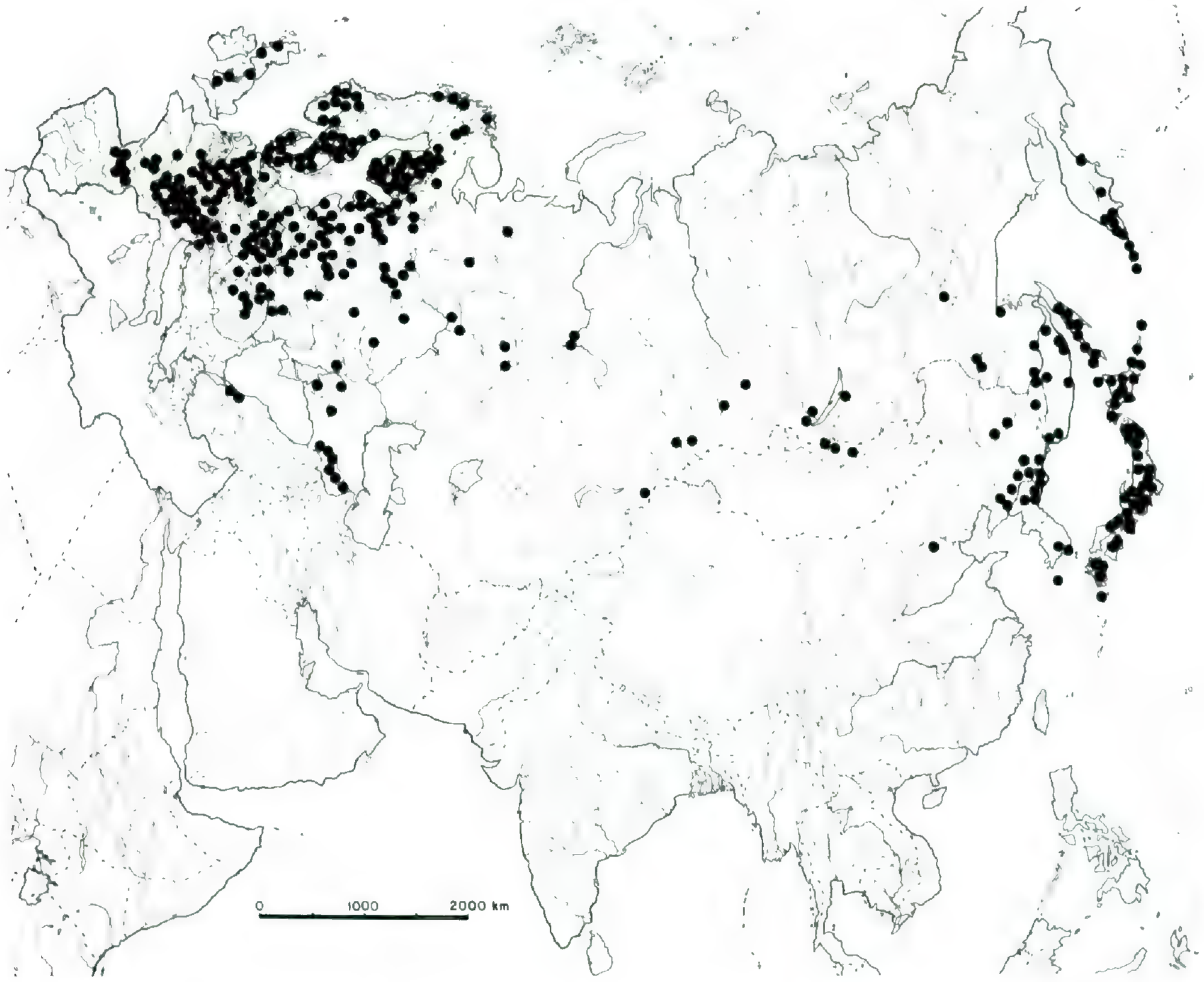


FIGURE 25. Distribution of *Circaea alpina* L. subsp. *alpina* in Eurasia.

Saskatchewan border, *M. G. Dumais & K. Anderson 3409* (ALTA, H, TRT); W side of Cold Lake on way to Marie Lake, *M. G. Dumais & K. Anderson 3507a* (ALTA); Big Island in Lake La Biche, *M. G. Dumais & K. Anderson 3637* (ALTA, CAN, TRT); Touchwood Lake, NE of Lake La Biche, *M. G. Dumais & K. Anderson 3696* (ALTA); ca. 2–3 mi. S of Fort Mackay, R. Mackay, *M. G. Dumais & K. Anderson 3877* (ALTA, CAN, DAO, TRT); 3 mi. E of Swan Hills, *M. G. Dumais & K. Anderson 4037* (ALTA); Waterton Lakes National Park, E slope of Mt. Crandall, *J. Kuijt & D. Dobbins 4434* (KESC); Castlemount, 8 mi. up W branch of Castlemount R., *M. O. Malte & W. R. Watson 2505* (CAN); W of Edmonton, near Winterburn, *W. C. McCalla E3555* (ALTA, UBC); W of Ellerslie, *E. H. Moss 1813* (ALTA); Edmonton, *E. H. Moss in 1944* (ALTA); Lesser Slave Lake, Faust, *E. H. Moss 6214* (ALTA); Lesser Slave Lake, Dog Island, *E. H. Moss 7919* (ALTA); Lesser Slave Lake, Widewater, *E. H. Moss 8268* (ALTA, DAO); Swan Hills, 25 mi. N of town, *J. G. Packer et al. 43* (DAO); vicinity of Fort McMurray, *H. Raup 7107* (CAN, GH, NY); Long Lake Provincial Park, *P. Scott & M. Dumais 1678* (CM, KYO, MHA, MO); 8 mi. W & 10 mi. N of Lacombe, *A. Sweet 10* (UAC); Fort Saskatchewan, *G. H. Turner 73* (GH); E of Pigeon Lake, near Mulhurst, *G. H. Turner 5029* (DAO); 55 mi. SW of Edmonton, near Mulhurst, *G. H. Turner 5029* (RSA); S of Battle Lake, 10 mi. SW of Ma-Me-O Beach on Pigeon Lake, *G. H. Turner 5946* (ALTA, CAN, DAO, MTJB); 6 mi. NE of Fort Saskatchewan, *G. H. Turner 739* (ALTA, DAO); Strathcona, *M. Willing in 1900* (SASK). BRITISH COLUMBIA: S Caribou Mts., Wells Gray Provincial Park, Murtle Lake, *L. & T. Ahti 6758* (H, V); Mara, *J. R. Anderson in 1904* (V); Comox Dist., Skeena, *J. R. Anderson in 1910* (WS); near mi. 284 of Alaska Hwy, *R. Annas in 1971* (UBC); Liard Hot Springs, mi. 496.5 of Alaska Hwy, *G. W. Argus & W. Chunys 5000* (CAN); Prince George Dist., Crooked R. below Davis Lake, *A. Auclair & S. Eis in 1963* (DAO); ca. 47 mi. N of Prince George, *A. Auclair 493* (DAO, MTMG, TRT); Summit Lake, ca. 25 mi. N of Prince George, *A. Auclair 519* (CAN, DAO, MTMG, TRT); Prince George Dist., 10 mi. N of Quesnel, *A. Auclair & S. Eis in 1963* (DAO); Wells area, Antler Creek, *K. Beamish et al. 8804* (UBC); 12 mi. E of Slocan Lake, Wilson Creek, *K. I. Beamish et al. 750249* (UBC); Chilcotin, *C. E. Beil 68-08-34* (UBC); Mabel Lake, *M. Bell in 1958* (UBC);

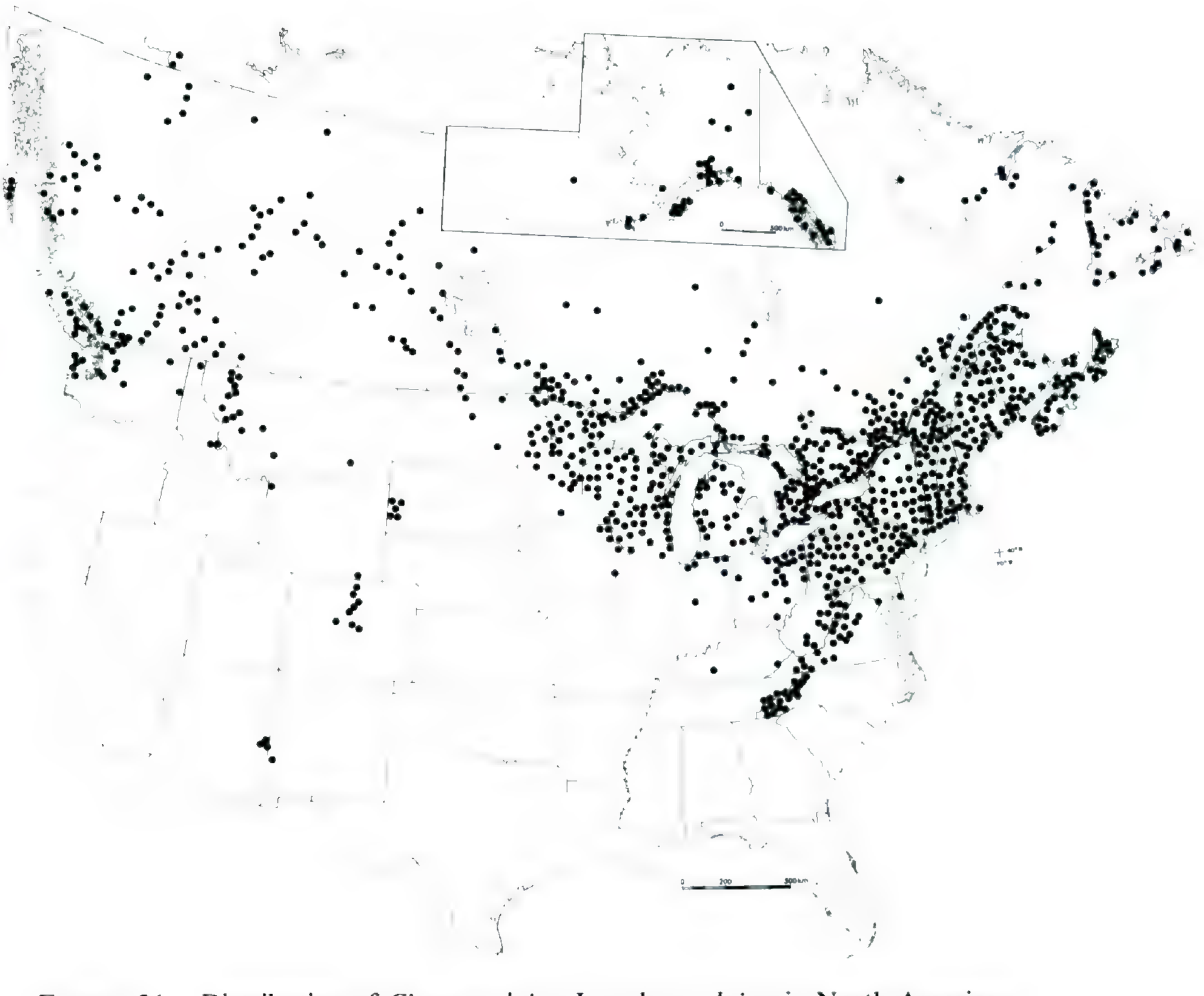


FIGURE 26. Distribution of *Circaea alpina* L. subsp. *alpina* in North America.

Othello, *T. C. Brayshaw 49218* (UBC); Ft. Nelson, *V. C. Brink in 1943* (UBC); Skeena Co., Prince Rupert, *H. H. Brown, in 1933* (DAO, TRT); 6 mi. SE of Nakusp on road to Denver, *J. A. Calder & D. Savile 9981* (NY, UBC, V); SE end of Lakelse, 11 mi. S of Terrace, *J. A. Calder et al. 13044* (CAS, DAO, GH, US); 3 mi. SW of Kwinitsa, *J. A. Calder et al. 13099* (COLO, DAO, UC); 16 mi. NNE of Barkerville along road to Bowron Lake, *J. A. Calder et al. 14310* (DAO, WTU); 6 mi. SW of Legate Creek–Skeena R. junction along road between Terrace & New Hazelton, *J. A. Calder et al. 14808* (DAO, UBC); from Williams Lake to Anahim Lake, *J. A. Calder et al. 17963* (DAO); 4.5 mi. E of Bella Coola on road to Anahim Lake, *J. A. Calder et al. 18510* (DAO, DS, UC); Martin Creek at mi. 242.5, Alaska Hwy, *J. A. Calder & I. Kukkonen 27137* (DAO, DS, MAK); Alaska Hwy, Liard Hot Springs, *J. A. Calder & I. Kukkonen 27557* (DAO); Queen Charlotte Islands, ca. 8 mi. SSW of Juskatla, *J. A. Calder & R. Taylor 35476* (DAO); 16 mi. S of Juskatla, *J. A. Calder & R. Taylor 35496* (DAO); Graham Island, N end of Long Aram, *J. A. Calder & R. Taylor 35968* (DAO); Queen Charlotte Islands, near W end of Mosquito Lake, *J. A. Calder & R. Taylor 36710* (ACAD, B, COLO, DAO, DS, GH, H, MAK, NCU, NY, OSC, RSA, SASK, TRT, TUR, UC, W, WS, WTU); Graham Island, W of Queen Charlotte City, *J. A. Calder & R. Taylor* (DAO); Pine R., near West Pine Bridge, *D. H. Calverley 224* (V); Mt. Robson Park, W entrance, *C. C. Chuang 75/91* (V); Jordan Creek near Revelstoke, *R. E. Cleland in 1921* (IND); Liard Hot Springs, 196 mi. NW of Fort Nelson, *R. F. Daubenmire 5152* (WS); Vancouver, Point Grey, *J. Davidson in 1911* (UBC); Brackendale, *J. Davidson in 1912* (UBC); Wigwam River, Kootanie Valley, *Dawson in 1883* (CAN); 5 mi. up Tzoonie R., *R. B. Dickens 131* (UBC); Canim Lake, Cariboo, *J. W. Eastham in 1946* (UBC); Fernie, Fairy Creek, *J. W. Eastham in 1947* (DAO, UBC, V); Glacier National Park, Glacier, *E. Farr in 1904* (PENN); Marysville, *F. Fodor 14* (UBC); Revelstoke, *F. Fyles in 1914* (DAO); Langley Prairie, *H. Groh in 1930* (DAO); Glacier National Park, Bald Mt. Trail to Grizzly Creek, *E. Haber & M. J. Shchepanek 1765* (CAN); Cathedral Park, junction of Ewart Creek and Ashnola R., *R. Hainault 7770* (UBC, V); Skagit Valley, Whitworth Ranch, *G. A. Hardy 20421* (V); Manning Park, *G. A. Hardy 21726* (V); Kooteway Dist., Crawford Bay, *L. C. Harrison s.n.* (WS); near Kitsault Glacier, Alice

Arm, *L. Harrison in 1949* (UBC); near Vancouver, *J. K. Henry 4242* (RM); Louise, *P. P. Henson in 1932* (DAO); Georgetown, *A. L. Hill in 1910* (UBC); Kinbasket Lake, *W. B. Johnstone in 1952* (V); Cultus Lake, *V. J. Krajina in 1949* (UBC) Cheam Lake, *V. J. Krajina 594* (DAO, GH, UBC, WIN); Vancouver Island, Nanaimo R. Valley, *V. J. Krajina et al. 4614* (DAO, GH, UBC); Vancouver Island, MacMillan Park, *V. J. Krajina et al. 5340* (DAO); ca. 10 mi. NNW of McGregor, *V. J. Krajina & J. Pojar in 1974* (UBC); 30 mi. SE of Purden Lake, Slim Creek, *V. J. Krajina et al. in 1974* (UBC); Hazelton, Vesterlund, *V. Kujala & A. Cajander in 1931* (H); Vancouver Island, Cowichan Lake, *V. Kujala & A. Cajander in 1931* (H); King Island, Port John, *H. M. Laing 585* (CAN); Bella Coola, Hagensborg, *H. M. Laing 586* (CAN); Agassiz, below Mt. Cheam, *G. F. Ledingham 49-498* (DAO); near Cheam R., *G. F. Ledingham & Brink 49-498* (USAS); Lower Fraser R., 49°N. Lat., *Dr. Lyall in 1859* (GH); Selkirk, N Fork Illecillawaet R., *J. Macmillan in 1904* (CM, NEB, PH, US); Cascade Mts., Yale, *J. Macoun 463* (MTMG); Chilliwack Valley, *J. M. Macoun 44410* (CAN, CAS, POM, WS); Agassiz, *M. O. Malte in 1912* (CAN); Bella Coola, *B. McAvoy 84* (UBC), *T. T. McCabe 1417* (UC); Fitzhugh Sound, Koeye R., *T. T. McCabe 3100* (UC); Swanson Bay, Graham Reach, *T. T. McCabe 3642* (UC); mainland opposite Kaun Island, *T. T. McCabe 4315* (UC); 8 mi. N of Revelstoke, Silvertip Falls, *T. T. McCabe 5453* (UC); Don Peninsula, Neekis R., *T. T. McCabe 7383* (UC); New Hazelton, *T. T. McCabe 8222* (UC, WTU); W of Vanderhoof, *A. P. McLaughlin 53* (V); Kitimat, *Mrs. G. Mendel 175* (V); 10 mi. NE of Terrace, Skeena Valley, *Mrs. G. Mendel 176* (V); Napieipuo R. Valley NE of 4th Lake, *D. Mueller-Dombois 98-5* (V); Mt. Waddington, Franklin Valley, *Mrs. D. Munday 9776* (V); Bouchie Lake, *J. A. Munro 241* (CAN); Crawford Bay, mouth of Crawford Creek, *H. Murray 16183* (DAO, UBC); Quesnal Dam, *W. A. Newcombe 405* (UBC, V); Yoe Island, Ellerslie Channel, *W. A. Newcombe in 1922* (V); 33 mi. N of Revelstoke near Mars Creek, *R. T. Ogilvie in 1953* (UBC); Aiyansh, *R. J. Pilfrey in 1960* (DAO); Klesilka R. near junction with Maselpanik Creek, *J. Pinder-Moss & P. Hamlyn 1168* (UBC); Liard Hot Springs, *A. & R. Porsild 22085* (CAN); vicinity of mouth of Quartz Creek, H. M. Raup & E. C. Abbe 4204 (CAN, GH, MIN, MT, NY, POM): near lower crossing of Liard R., *H. M. Raup & D. S. Correll 10888* (A, CAN, UBC); Mckinley Lake, 20 mi. SE of Horsefly, *S. Russell 8-M* (V); Graham Island, Blackwater Creek, Juskatta area, *D. B. O. Savile 3527* (DAO); Mt. Robson, *E. Scammon 3303* (GH); Front Lake City, *E. Scheuber in 1904* (US); N of Terrace, W side of Kitsumgallum Valley, *R. L. Schmidt 37* (UBC); Selkirk, near Nelson, *C. H. Shaw 665* (CM, COLO, GH, NEB, NY, PH, US); Selkirk, woods by Goldstream, *C. H. Shaw 1085* (CM, COLO, GH, GRI, MO, NEB, NY, PENN, PH, US); Selkirk, near mouth of Downie Creek, *C. H. Shaw 1120* (CM, COLO, GH, GRI, MO, NEB, NY, PENN, PH, US); Mt. Revelstoke National Park, W Woolsey Creek, *J. H. Soper & M. J. Shchepanek 12793* (CAN, V); Chilliwack Valley, *J. Sprendborough 79405* (CM); Vancouver Island, Renfrew Dist., *C. Rosendahl 834* (CAN, COLO, DS, MIN, MO, NEB, NY, RM); Horseshoe Valley, Stillwater, *G. Stanley B222* (V); Bear Creek, Penticton, *M. Stonor in 1937* (UBC); foot of Mt. Robeson along rte 16, *G. B. Straley 1621* (MO); along rte 24, ca. 6 mi. W of Little Fort, *G. B. Straley 1649* (MO); 20 mi. E of Revelstoke, Illacillewaet R. on border of Glacier National Park, *A. F. Szczawinski in 1964* (DAO, UBC, V); 2 mi. W of Brisco, *R. L. Taylor & D. H. Ferguson 2530* (DAO, DS); 4.5 mi WSW of Wycliffe, *R. L. Taylor & D. H. Ferguson 2636* (DAO); 4.3 mi. S of Grindrod on hwy 97E, *R. L. Taylor & G. Staudt 4314* (DAO, NY); Victoria Island, Markale, Kyuquot, *T. M. C. Taylor & A. F. Szczawinski 259* (UBC, V); Stanley, *T. M. C. Taylor 9055* (UBC); Mt. Waddington, *W. Taylor in 1937* (UBC); 100 mi. N of Golden, *W. A. Weber 2528* (CAN, COLO, GH, NY, POM, UBC, UC, V, WS, WTU); Armstrong, Okanagan, *E. Wilson 229* (UBC). LABRADOR: Foot of Big Hill portage, Hamilton R., *M. T. Doutt 3243a* (CM); Straits of Belle Isle, Forteau, *M. L. Fernald & K. M. Wiegand 3747* (CU, GH); Goose Bay, *J. M. Gillett & W. I. Findlay 5547* (DAO, MIN, RM, UBC, WS, WTU); Traverspine R., *J. M. Gillett & W. I. Findlay 5610* (ACAD, DAO, GH, MT, NY, TRT, US, W); Kenemich R., *J. M. Gillett & I. McKay 5814* (DAO); Hamilton R., Twin Falls area, *I. Hustich & P. Kallio 139a* (TUR); Northwest River area, Salt Pond, *I. Hustich & P. Kallio 476* (TUR); Schefferville area, Knob Lake, *I. Hustich & P. Kallio 833* (TUR); Goose Bay, *W. Schofield 687* (DAO); Capstan Island, *A. C. Waghorne in 1893* (KSC, MIN, US). MANITOBA: Otterburne, to the E, *Fr. J. P. Bernard 58/386* (MT); MacDonald Dist., 3 mi. SW of Shilo, *B. Boivin et al. 13199* (DAO, GH, NY, WIN); Max Lake, Turtle Mts., *M. v. Buskirk M-9* (WIN); Lake of Woods, *G. Dawson in 1873* (MTMG, TRT); Sandy Hook, *M. G. Dudley in 1929* (WIN); Swan R., *H. Groh in 1922* (WIN); Gimli, *V. W. Jackson in 1923* (WIN); Porcupine Provincial Forest, *G. M. Keleher 71-25* (WIN); The Pas, Lake Atibameg area, 25 mi. N, *W. Krivda 1523* (UBC); The Pas, Preachart's woods, *W. Krivda 66-575* (MAK); The Pas, Rall's Island, *W. Krivda 72-571* (WIN); Pinawa, F. I. G. Area, Whiteshell Nuclear Research Establishment, *R. E. Longton in 1977* (WIN); NW of Grassy Narrows, S19, T24, R5E, *A. & D Löve 5492* (DAO, NDA, US, WIN); Camp Morton, S9, T20, R4E, *A. & D. Löve 5708* (CAN, DAO, MTJB, SASK, US, WIN); Shoal Lake, *C. W. Lowe in 1921* (WIN); Dog-head, Lake Winnipeg, *J. M. Macoun in 1884* (CAN); Brandon Dist., Brandon, *H. Marshall 54* (DAO); Brokenhead, S35, T14, R7, *T. Mosquin in 1952* (DAO, WIN); Gilbert Plains, *J. L. Parker 2945* (WIN); Riding Mountain National Park, *J.*

Rowe in 1948 (WIN); Lake Winnipegosis, Nason Island, N of Whiteaves Point, Dawson Bay, *H. J. Scoggan 4588* (CAN, UBC, WIN); Herb Lake, around village on Wekusko Lake, *H. J. Scoggan 6476A* (ALTA, CAN); Lake Winnipeg, Hecla Island, *H. J. Scoggan 9136* (ALTA, CAN, GH, MIN, MT, WIN); Brandon, *G. A. Stevenson 1506* (DAO, NDA). NEW BRUNSWICK. Sunbury Co., Acadia Forest Experiment Station, *G. C. C. in 1957* (UNB); Kings Co., Hampton, *A. Chadbourne in 1883* (GH); Campbellton, *R. Chalmers in 1877* (CAN); Kings Co., Quoddy Bay, Indian Island, *M. Chrysler 6075* (GH); Quoddy Bay, Deer Island, *M. Chrysler 6115* (GH); Northumberland Co., Bay du Vin, *P. Cox in 1908* (UNB); St. Andrews, *E. H. Craigie in 1914* (TRT); Carleton Co., Richmond Corner, *W. G. Dore & E. Gorham 45857* (DAO, MT, NHA, US); Carleton Co., W of Woodstock, *W. G. Dore & E. Gorham 45915* (DAO, MT); York Co., Oromocto R., *B. Ellis 63-47* (UNB); Queens Co., Charlottetown, *M. L. Fernald et al. 7838* (GH); St. Andrews, *J. Fowler in 1900* (US); Charlotte Co., Kent's Island, *H. Gleason 89* (NY); Bay of Fundy, Kent's Island, *H. A. Gleason, Jr. 14* (NY, WVA); Restigouche Co., Summit Depot, *R. H. 735* (UNB); Fredericton, Odell Woods, *Hagmeier in 1958* (DAO, UNB); St. John, Lily Lake, *G. U. Hay 207* (ACAD); Carleton Co., near Jackson Falls, *K. Heinstein in 1965* (UNB); Charlotte Co., S Wolf Island, *A. R. Hodgdon & R. B. Pike 18074* (NHA, UNB); Kings Co., Shediac Cape, Bateman's Pond, *F. Hubbard in 1914* (GH); Kings Co., Albert, *C. Knowlton in 1925* (GH); Fundy National Park, Point Wolfe R., *T. M. Lothian 155* (DAO); St. Andrews, *M. O. Malte 149/29* (UTC, WTU), *M. O. Malte 192/29* (CAN); Bathurst & vicinity, *M. O. Malte 648* (CAN, WTU); St. Leonard & vicinity, *M. O. Malte & W. R. Watson 501* (CAN, WS, WTU); Blue Bell Mt., *M. O. Malte & W. R. Watson 682* (CAN, WS); Sunbury Co., near Fredericton, *C. McKenney 5,6-25* (BH, DAO, MIN, MONTU, MT, NA, NY); Balhurst, *L. Meehan in 1869* (MTMG); Grand Manan Island, N Head, *A. E. Perkins in 1935* (CU); Carlton Co., Tracey Mills, *H. G. Perry in 1910* (ACAD); St. Andrews, Biological Station, *H. G. Perry in 1913* (ACAD); 1 mi. SW of Tay Mills, *W. H. Poole 296* (DAO); Carleton Co., Hartland, *P. R. Roberts 60-257* (UNB); York Co., near Moose Lake, *P. R. Roberts & D. E. Drury 63-1186* (ACAD, MT, UNB); Madawaska Co., rte 7, from Black Brook, *P. R. Roberts & D. E. Drury 63-1718* (UNB); Victoria Co., Grand Falls, *P. R. Roberts & D. E. Drury 63-1549* (DAO, UNB); Restigouche Co., States Lake, *P. R. Roberts & D. E. Drury 63-1855* (UNB); Northumberland Co., Burnt Church R. at hwy bridge over #11, *P. R. Roberts & D. E. Drury 63-2079* (DAO, UNB); Madawaska Co., road to Long Sett from Clair, *P. R. Roberts & N. Bateman 64-3188* (DAO, UNB); Victoria Co., Wapskehegan R. at E Beaver Brook, *P. R. Roberts & N. Bateman 64-3589* (CAN, UNB); Victoria Co., between dammed Long Lake & Mud Lake, *P. R. Roberts & N. Bateman 64-3701* (DAO, UNB); Restigouche Co., Kedgwick R. at Mile Brook, *P. R. Roberts & N. Bateman 64-3886A* (UNB); Northumberland Co., 5 mi. W of Red Rock, *P. R. Roberts & B. Pugh 65-1414* (UNB); Kent Co., 1.5 mi. S of S St. Nicholas, *P. R. Roberts & B. Pugh 65-2332* (MT, UNB); Kent Co., 4 mi. N of Bass River Settlement, *P. R. Roberts & B. Pugh 65-2426* (UNB); Restigouche Co., Tetagouche R. between Lower & Middle Tetagouche Lakes, *P. R. Roberts & B. Pugh 65-5003* (UNB); Retigouche Co., Jacquet River Lake, *P. R. Roberts & B. Pugh 65-5056* (UNB); Restigouche Co., Tetagouche R. headwaters, *P. R. Roberts & B. Pugh 65-5099* (UNB); Gloucester Co., Tetagouche Falls, *P. R. Roberts & B. Pugh 65-5236* (UNB); Restigouche Co., N Branch Charlo R., *P. R. Roberts & B. Pugh 65-5510* (UNB); Restigouche Co., junction of Little Popelogan and SE Upsalquitch Rivers, *P. R. Roberts & B. Pugh 65-5848* (UNB); Victoria Co., Moose Mt. Fire Tower, *P. R. Roberts & B. Pugh 65-6191* (UNB); Restigouche Co., E end of Little Nictor Lake, *P. R. Roberts & B. Pugh 65-6267* (UNB); St. John Co., Cape Spencer, *P. R. Roberts & B. Pugh 65-6344* (UNB); Restigouche Co., Miner's Road along Portage Lake, *P. R. Roberts 66-488* (UNB); York Co., Maple Grove, *P. R. Roberts 66-673* (UNB); Charlotte Co., St. Andrews, *D. R. Sampson 173* (MT); Fredericton, *H. J. Scoggan 12816* (ACAD, CAN, MAK, W); ca. 25 mi. SW of Campbellton, Squaw Cap, *H. J. Scoggan 13125* (CAN); Sussex, ca. 45 mi. SW of Moncton, *H. J. Scoggan 13417* (ACAD, MAK, W); Restigouche Co., 8 mi. SW of Nictau Lake, *E. C. Smith & R. E. Clattenburg 20037* (ACAD); York Co., 0.75 mi. W of Hanville, *E. C. Smith & J. M. Stanley 23355* (ACAD); Restigouche Co., Summit Depot, *E. C. Smith et al. 16235* (ACAD); Northumberland Co., Tabusintoc R., *E. C. Smith et al. 16488* (ACAD); Campobello Island, *J. Smith 767* (US); Fawcett Hill, *W. A. Squires & D. Christie in 1963* (DAO); woods S of The Whistle, Grand Manan, *C. A. & U. E. Weatherby, Pl. Exs. Grayanae 1079* (ARIZ, B, BH, CAN, CAS, COLO, DAO, DS, GA, GH, IA, ILL, IND, ISC, KY, LL, LTU, MASS, MICH, MIN, MO, MONTU, MT, NA, NCSC, NCU, NHA, NY, NYS, OKL, OKLA, OSC, PAC, PENN, PH, POM, RM, SMU, TENN, TEX, TNS, TRT, UARK, UC, US, UTC, WIS, WS, WTU, WVA); Cape Breton Island, New Campbelltown, *D. White & C. Schuchert 65* (US); York Co., near Scotch Lake, *without collector 798* (UNB); Madawaska Co., 3rd Lake, Green R., *without collector in 1957* (UNB). NEWFOUNDLAND: Bay of Islands, *D. A. Atkinson in 1907* (CM); S of Gander, Gander Lakes, *I. Basset 439* (DAO, MO, MT); 1 mi. SW of Cartyville, *I. Basset 730* (DAO); Neddy Harbor, near Bonne Bay, *H. Bishop 438* (CAN, GH); Western Brook Pond, *A. Bouchard & G. Hay 72-372* (CAN); St. Paul's Inlet, *A. Bouchard & G. Hay 72-373* (CAN); St. Barbe S Dist., Gros Morne National Park, Lobster Cove Head, *A. Bouchard & S. G.*

Hay 72-374 (MT); near Hawke Bay, *J. Donly 49* (DAO); Bay of Islands, *E. H. Eames & C. C. Godfrey 7054* (IND); Humber Arm Region, Birchy Cove (Curling), *M. L. Fernald & K. M. Wiegand 3746* (CU, GH, NY, PH); Region of Ingornachoix Bay, Port Saunders, *M. L. Fernald & K. M. Wiegand 3748* (CAN, CU, GH); S shore of Notre Dame Bay, Black Island, *M. L. Fernald & K. M. Wiegand 5935* (GH, PH); W (S) Arm Bonne Bay, near Winterhouse Brook, *M. L. Fernald et al. 1888* (GH, PENN, US); Straits of Belle Isle, Mistaken Cove, *M. L. Fernald et al. 26844* (CU, GH, PH); Bay of Islands region, Mt. Moriah, *M. L. Fernald et al. 26845* (CU, GH, NY, PH, US); 3 mi. SE of Argentina, *D. Grether 7758* (DAO, WIS); La Poille Bay, Bay du Nord village, *A. Heyl 116* (PH); Placentia East Co., Southern Harbor, *J. H. Himmelman 109* (ACAD); Channel, *C. Howe & W. Lang 888* (GH, NY); Conception Bay, near Topsail, *C. Howe & W. Lang 1223* (GH, NY); Bonne Bay, above Woody Point, *R. Kimball 117* (GH); near Frenchman's Cove, *K. K. Mackenzie 10358* (GH, NY); Humber Dist., Big Falls, Upper Humber R., *D. Pimlot 212* (MT, WIS); Flower's Cove, *M. Priest in 1920* (GH); Manuels R., *B. L. Robinson & H. Schrenk 6* (CAN, GH, MIN, MO, NY, PH, US); Doncette Brook, Tompkins, *A. E. Roland & E. C. Smith 74* (ACAD); Humber Dist., Goose Arm, E of William Wheeler Point, *E. Rouleau 137* (DAO, MT); Humber Dist., Steady Brook, *E. Rouleau 762* (DAO, MT); Humber Dist., Grand Lake, Hinds Brook Falls, *E. Rouleau 2257* (MT); Burin Dist., Main R., *E. Rouleau 4213* (DAO, MT); Barbe Dist., 4 mi. N of Cow Head, Stanford or Slants R., *E. Rouleau 4344* (MT); ca. 1 mi. S of Loon Bay, *E. Rouleau 4863* (DAO, MT, US); St. Georges Dist., Mollichiogneck Brook at the junction of Great Codrey R., *E. Rouleau 6482* (MT); Fortune Bay–Hermitage Dist., Grand-le-Pierre, *E. Rouleau 6820* (MT); Englee, *D. Savile 2708* (DAO); St. Anthony, *D. Savile 2931* (DAO); Port au Choix, *D. Savile 3033* (DAO); Bonavista North, Alexander Bay, Thimble Cove, *A. Smith et al. 220* (DAO); Lewisport, *J. Sornborger in 1903* (GH); Cow Head, *H. J. Squires 156* (ACAD); Salmonier, *R. Thaxter in 1885* (GH); Coal R., *A. C. Waghorne in 1896* (MO); Capstan Head, *A. Waghorne in 1893* (NY); Straits of Belle Isle, Sacred Island, *K. M. Wiegand et al. 28747* (CU, GH, PH); Placentia, Avalon Peninsula, *C. Williamson 328* (NY, PENN, PH). NORTHWEST TERRITORIES: Mackenzie Dist., 8 mi. SW of Fort Liard, *W. J. Cody & K. W. Spicer 11638* (MO, SASK, SMU, UBC); Mackenzie Dist., Big Island, 15 mi. N of Fort Liard, *W. J. Cody & K. W. Spicer 11834* (ALTA, MAK, MICH, MIN, NY); Mackenzie Lowlands, Liard R. valley, *W. Jeffrey 20* (CAN); Mackenzie Dist., Reed's Portage, Upper Embarras R., *H. Raup 2843* (CAN, H, NY, UC, US). NOVA SCOTIA: Sandy Cove, *J. Adams in 1937* (DAO); Cape Breton, Pleasant Bay, *L. H. & E. Z. Bailey 593* (BH); Annapolis Co., North Mt., Granville, *E. Bartram & B. Long 24216* (CAN, GH, PENN); Colchester Co., Folleigh, *R. C. Bean et al. 22007* (GH); Colchester Co., Salmon R., Bible Hill, near Truro, *H. P. Bell et al. in 1949* (DAL); Halifax Co., Kearney Lake, *H. P. Bell et al. in 1949* (DAL); Queens Co., Port Mouton, *H. P. Bell et al. 50226* (DAL); Colchester Co., Truro, *C. Bissell & C. Linder 22006* (CAN, GH, PENN); Colchester Co., 3 mi. NW of Kemptown, *B. Brown in 1972* (MTMG); Five Islands, R., *E. Chase in 1960* (DAO); Antigonish, Frasers Mill, *H. L. Christie 12365* (ACAD); Colchester Co., Central New Annan, *W. Cody 21494* (DAO, MO); Shelburne Co., Bon Portage Island, Cranberry Swamp, *G. Demone 23529A* (ACAD); Pictou Co., near Scotsburn, Roger Hill, *W. G. Dore & E. Gorham 45449* (ACAD, DAL, DAO, LL, MT); Kings Co., Hunting Point, *J. S. Erskine in 1949* (DAL); Kings Co., E of White Rock dam, *J. S. & D. Erskine 178* (ACAD); Annapolis Co., near Margaretsville, *J. S. & D. Erskine 311* (ACAD); St. Paul Island, Little Lake, *J. S. Erskine 53916* (DAO, MTJB); Yarmouth Co., Tusket Islands, Owl Head, *J. S. Erskine 54-1378* (ACAD); Victoria Co., North River, *J. S. Erskine & P. Bentley 56316* (DAO); Yarmouth Co., Mud Island, *J. S. Erskine 56675* (ACAD); Cape Breton, Wycocomagh, Sky Mt., *D. Etheridge 614* (UNB); Guysboro Co., Glenelg, *E. R. Faribault 817* (MT); Cape Breton Highlands National Park, S Ingonish, *H. Ferguson 1-4-43* (DAO, NY, WIS); Queens Co., near mouth of Broad R., *M. L. Fernald & C. Bissell 22011* (GH, PENN); Queens Co., Keji National Park, W of Grafton Lake, *H. L. Forsyth in 1972* (ACAD); Canso, *J. Fowler in 1901* (UBC, UNB); Chezzetcook, *M. Forward in 1930* (UBC); Digby Co., between Meteghan & Belliveau, *J. Gillett & J. Soper 15705* (CAN); Digby Co., Brier Island, *D. P. Gordon in 1972* (DAL); Cumberland Co., Soldier Brook, Refuge Cove, *M. J. Harvey in 1978* (DAL); Halifax Co., White Island, *W. S. Hoar in 1939* (TRT); near Digby, *C. Howe & W. Lang 167, 259* (GH, NY); Pictou Co., near Pictou, *C. Howe & W. Lang 509* (GH, NY); Annapolis Co., Karsdale, *J. W. Johnson in 1962* (ACAD); Willowdale, *J. T. B. K. in 1947* (UNB); Halifax Co., Lakeview, *H. M. King in 1901* (DAL); Kings Co., Lakeville, *R. M. Lewis & E. Gorham in 1944* (DAL); Kings Co., Canaan, *R. M. Lewis 1627* (DAO); Annapolis Co., N of Middleton, North Mt., *B. Long 22009* (GH, PH); Yarmouth Co., Beaver Lake, *B. Long & D. Linder 22010* (CAN, GH, PH); Blomidon, *J. Macoun 2010* (CAN); Cape Breton Island, Baddeck, *J. Macoun 19127* (CAN, GH); Colchester Co., Salmon R. near Truro Agr. College, *S. Mason et al. 197* (DAO); Halifax Co., Kearney's Lake, *J. W. McLellan in 1937* (DAL); Cape Breton, *G. Nichols 986* (GH); vicinity of Guysborough, *H. Osborn in 1879* (DAO); Cumberland Co., Springhill Junction, *A. S. Pease & B. Long 22005* (GH, PH); Hants Co., Five Mile R., *A. S. Pease & B. Long 22008* (PH); St. Paul Island, Coggin Mt., *L. Perry & M. Roscoe 292* (CAN, GH, MT, PH); Guysborough Co., West Cook's Cove, *N. G. Perry et al. 10110* (ACAD); Kent's Island, S end, *D. Potter 5030* (TRT); Colches-

ter Co., Folleigh Lake, *A. R. Prince & C. E. Atwood 277* (DS, MICH); Colchester Co., Lower Five Islands, *A. R. Prince & C. E. Atwood 1128* (DAO, DS); Cumberland Co., Tidnish, *C. H. Read 12282* (ACAD); Inverness Co., Whycocomagh Indian Reservation no. 2, *P. R. Roberts 59-936* (UNB); Pictou Co., Bayview, *C. Robinson 216* (NY); Digby Co., Brier Island, *Roland et al. 137* (ACAD); Yarmouth Co., Carleton, *M. V. Roscoe et al. 11073* (ACAD, DAL, MT, TRT); Digby Co., Sandy Cove, *M. V. Roscoe & J. E. Graustein 11074* (ACAD); Guysborough Co., Guysborough, *J. Rousseau 35351* (CAN, MT); Cape Breton, Victoria Co., Port Bevis, *E. Scammon 4380* (GH); Cape Breton Co., Grand Narrows, *E. Scammon 4381* (GH, MIN); Digby Co., Brier Island, *W. B. Schofield 1661* (MT); Cumberland Co., New Prospect, *W. B. Schofield 3156* (ACAD); Cumberland Co., Isle au Haute, *W. B. Schofield 3747* (ACAD); Cumberland, Lake Killarney, *W. B. Schofield 4154* (ACAD); Colchester Co., Moose Island, *W. B. Schofield 5012* (ACAD); Grand Manan, *W. Seaman s.n.* (MTMG); Brier Island, *E. C. Smith et al. 137* (DAO); Richmond Co., Roberta, *E. C. Smith et al. 722* (ACAD); Inverness Co., Red River, *E. C. Smith et al. 1104* (ACAD); Victoria Co., Salmon R., *E. C. Smith et al. 2654* (ACAD, DAO, MT, NCSC); Antigonish Co., Keppoch, *E. C. Smith et al. 2891* (ACAD, DAO); Victoria Co., Cape North, *E. C. Smith et al. 3722* (ACAD); Victoria Co., Ingonish R., *E. C. Smith et al. 4318* (ACAD, MT); Inverness Co., Glendyer, *E. C. Smith et al. 4782* (ACAD, MT, TRT); Richmond Co., Loch Lomand, *E. C. Smith et al. 5424* (ACAD); Inverness Co., 4 mi. W of Big Southwest Brook, *E. C. Smith et al. 6531* (ACAD, MT); Inverness Co., Cheticamp R., *E. C. Smith et al. 7811* (ACAD, MT); Victoria Co., Indian Brook, *E. C. Smith et al. 8131* (ACAD, TRT); Cape Breton Co., North Light, Scatari, *E. C. Smith et al. 8473* (ACAD, DAO); Inverness Co., Skye Glen, *E. C. Smith et al. 8676* (ACAD, DAO, TRT); Lunenburg Co., Horseshoe Lake, *E. C. Smith et al. 8990* (ACAD, MT); Inverness Co., Cape St. Lawrence, *E. C. Smith et al. 11143* (ACAD); Queens Co., W of Eighth Lake, *E. C. Smith et al. 11802* (ACAD); Digby Co., Cedarwood Lake, *E. C. Smith et al. 15321* (ACAD); Victoria Co., Middle Branch of North R., "Big Lease," *E. C. Smith et al. 16756* (ACAD); Richmond Co., Pringles Mt., *E. C. Smith et al. 17788* (ACAD, DAO); Pictou Co., Brookland, *E. C. Smith et al. 18152* (ACAD, DAO); Guysborough Co., Salmon River Lake, *E. C. Smith et al. 18228* (ACAD); Colchester Co., West Branch, North R., *E. C. Smith et al. 18975A* (TRT); Colchester Co., Byer's Brook, *E. C. Smith et al. 19037* (ACAD, MT); Inverness Co., Sight Point, *E. C. Smith et al. 21113* (ACAD); Lunenburg Co., Crousetown, *E. C. Smith et al. 21253* (ACAD); 4 mi. E of Halls Harbor, *E. C. Smith et al. 23262* (DAO); Hants Co., E of Minasville, *E. C. Smith et al. 23570* (ACAD); Kings Co., Amethyst Cove, *P. C. Smith 210* (ACAD); Pictou Co., Springville, *H. St. John 1435* (CAN, CAS, GH, ISC, MIN, MT, US, WS); Inverness Co., Cape Breton Highlands National Park, McIntosh Brook Picnic Site, *L. J. Uttal 7451* (VPI); Hants Co., W Gore, *F. Wallace 86* (MTMG); Truro, Victoria Park, *R. Witmore in 1919* (MTMG); Kings Co., Cape Split, *M. N. Zinck 282* (DAO); Kings Co., near Summit Lake, *M. N. Zinck 632* (DAO). ONTARIO: Grimsley, *C. Armstrong in 1892* (US); Nipissing Dist., Algonquin Park, near Lake of Two Rivers, *P. Bahr in 1963* (MTMG); Thunder Bay Dist., Sibley Provincial Park, *J. A. Bailey 1047* (TRT, V); Thunder Bay Dist., Oliver Twp, Kakabeka Falls, *J. A. Bailey 1808* (TRT, WTU); Thunder Bay Dist., Sibley Peninsula, N end of Lake Marie Louise, *J. A. Bailey 2496* (V); Timiskaming Dist., New Liskeard, 3 mi. E in Harris Twp, *W. K. W. Baldwin 5205* (CAN, SASK, TRT); Kenora Dist., Sandybeach Lake, *W. K. W. Baldwin 8507* (TRT); Kenora Dist., Ignace, *W. K. W. Baldwin 9009* (CAN, H, MIN, TRT); Thunder Bay Dist., Allan Water R., inlet river from Kawaweogama Lake, *W. K. W. Baldwin 9201* Cochrane Dist., Matheson, *W. K. W. Baldwin & A. J. Breitung 3233* (CAN, H, TRT, WIN); Cochrane Dist., Mammamattawa, Kenogami R., *W. K. W. Baldwin et al. 6424* (CAN); Cochrane Dist., junction of Mattagami & Missinaibi Rivers, *W. K. W. Baldwin & A. Porsild 7312* (CAN); Black Sturgeon Lake, *R. L. Beacroft in 1950* (HAM); Kenora Dist., Blacky Bay, S shore of Kakagi Lake, *P. Bentley 57513* (CAN, DAO, MTMG); Carleton Co., Gloucester, *B. Billings in 1866* (NA); near Toronto, *Biltmore Herb. in 1897* (US); Petawana Forest Experiment Station, *E. Blair 10-140* (NA); Peterborough Co., 2 mi. N of Havelock, *R. S. Bobbette 4358* (CAN); Grey Co., 2.5 mi SE of Eugenia, *R. S. Bobbette 4873* (CAN); Algoma Dist., Agawa R. at rte 17, *D. E. Boufford 18744* (KYO, MHA, MO); Algoma Dist., 0.9 mi. N of Gravel R. on rte 129, *D. E. Boufford 18783* (MO); Sudbury Dist., 8.2 mi. N of the Manitoulin Dist. line on rte 68, *D. E. Boufford 18802* (MO); Manitoulin Dist., 6.8 mi. N of the ferry and the S end of hwy 68 on hwy 68, *D. E. Boufford 18803* (KYO, MO); Grey Co., ca. 5 mi. N of Durham, *D. E. Boufford 18813* (BM, CM, K, KYO, MHA, MO, P, PE); Turkey Point, Lake Erie, *W. M. Bowden in 1935* (HAM); Martin R., Sisk, *W. B. Brierly & W. H. Hodge 633* (TRT); York Co., Kettleby Kabin near Schamberg, *H. H. Brown in 1925* (CAN); York Co., Pottageville, *H. H. Brown in 1929* (TRT); Peel Co., Credit Forks, *H. H. Brown in 1929* (TRT); Leeds Co., Westport, *H. H. Brown 4232* (TRT); Kenora, *A. H. R. Buller in 1918* (WIN); London, *T. Burgess in 1879* (MTMG); Dundas, Dundas Ravine, *T. Burgess in 1888* (HAM); Brant Co., New Durham, *R. F. Cain 208* (TRT, W); Ontario Co., ca. 2.5 mi. N of Leaskdale, Scott Twp, *P. M. Catling & S. McKay in 1970* (TRT); Algoma Dist., near Pancake R., near Lake Superior shore, *P. M. Catling et al. in 1975* (TRT); Russell Co., Cumberland Twp, *W. Cody & J. Calder 554* (DAO, KANU); Victoria Co., Laxton Twp, 3 mi. W of Norland, *M. Cody & J. Parmelee 6665* (DAO); Port Carling, *L. C. Coleman in 1940*

(TRT); Haliburton Co., Harburn Twp, *V. Connolly 207* (TRT); Thistletown, *F. S. Cook in 1948* (TRT); Thunder Bay Dist., Oliver Twp, *Cormack & Mayall in 1936* (MICH); Thunder Bay Dist., Victoria Island, Thunder Bay, *Cormack & Mayall in 1936* (TRT); Algoma Dist., Lake Superior Provincial Park, Old Woman Bay, *F. N. Cowell 154* (DAO); Algoma Dist., hwy 17, Lake Superior Provincial Park, *F. N. Cowell 262* (TRT); Thunder Bay Dist., Lake Nipigon, Geikie Island, *A. Gringan 144* (TRT); Patricia Dist., island in Nikip Lake, *A. T. Cringan P140* (TRT); Norfolk Co., Charlotteville Twp, Turkey Point, *J. E. Cruise 6298* (CU, TRT); near Lake of the Woods, *G. M. Dawson in 1873* (CAN); Ingolf, *W. Denike 549* (DAO, NA); Victoria Co., Bexley Twp, ca. 4 mi. SW of Coboconk, *W. S. Dickinson 104* (CAN, DAO, TRT); Victoria Co., Laxton Twp, ca. 2 mi. NW of Norland, *W. S. Dickinson 127* (CAN, DAO, TRT); Simcoe Co., Vespra Twp, ca. 7 mi. W of Barrie, *W. S. Dickinson et al. 441A* (CAN, DAO, MTMG, NCU, TRT); Parry Sound Co., Hagerman Twp, Lorimer Lake, *W. S. Dickinson 485* (CAN, DAO, MTMG, NCU, TRT); Cochrane Co., Horden Twp, ca. 2 mi. S of Moosonee, *W. S. Dickinson & E. Haber 504* (CAN, DAO, TRT); Leeds Co., Otter Lake near Lombardy, *W. Dore & W. Cody 47-389* (DAO); Frontenac Co., Sharbot Lake, *W. Dore & J. Gillett 13861* (DAO); Greenville Co., 2.3 mi. N, 15°W of Prescott, *W. Dore et al. 17827* (DAO, TRT); Northumberland Co., S of Brighton, *M. Dumais 255* (DAO, TRT); Leeds Co., Oliver's Ferry, Rideau Park, *T. Edmonson in 1898* (NY); Haley's Station, *T. Edmonson 2589* (NY); Leeds Co., Rideau Ferry, *T. Edmonson 2879* (NY); Port Stanley, *G. L. Fisher in 1909* (OKLA); Muskoka Co., Lumina, Lake of Bays, *M. J. Fisher in 1925* (CU); Huron Co., Grey Twp, 8.5 mi. E of Brussels, *G. Fleischmann 125* (DAO); Beechwood, *J. Fletcher 863* (PH); Plevna, *J. Fowler in 1902* (CAN, DAO, GH); Peel Co., Caledon Lake, *L. Gad in 1971* (TRT); Durham Co., Darlington Twp, N of Haydon, *L. Gad et al. in 1974* (TRT); Thunder Bay Dist., N side of Grass Lake, Sibley Peninsula, *C. E. Garton et al. 1337* (DAO, MIN, MT, TRT, US, WIS); Thunder Bay Dist., NE corner of Roundtable Lake, Hardwick Twp, *C. E. Garton 1481* (DAO, MIN, MT, PENN, SDU, TRT, TUR, W, WIN); Thunder Bay Dist., SE of Lenore Lake, Pardee Twp, *C. E. Garton 1919* (DAO, GH, H, MIN, NY, RM, TRT, UC, US, W, WIN); Thunder Bay Dist., 0.25 mi. W of Perrys Bay, Sibley Twp, *C. E. Garton 2239* (DAO); Rainy River Dist., French Lake Headquarters (Quetico), *C. E. Garton 4742* (DAO, MT, TRT); Thunder Bay Dist., S side of St. Ignace Island, *C. E. Garton 6406* (DAO, NCU, TRT); Thunder Bay Dist., SW corner of St. Ignace Island, NE corner of Squaw Bay, *C. E. Garton 6637* (DAO, GH, H); Thunder Bay Dist., Kilkenny Twp, MacDiarmid, *C. E. Garton 7661* (DAO, MAK, TRT); Thunder Bay Dist., Lake Nipigon, Cooke Point, *C. E. Garton 7793* (ALTA, DAO); Rainy River Dist., 5.5 mi. below Rainy River town, *C. E. Garton 8682* (DAO, UC); Rainy River Dist., Duke Twp, E of Pinewood, *C. E. Garton 9640* (DAO, MASS, MIN, SASK, TRT); Thunder Bay Dist., Dorion Twp, Coldwater Creek at Black Bay, *C. E. Garton 9633* (CM, DAO, TRT); Thunder Bay Dist., 9.3 mi. N of Black Sturgeon Ranger Station, *C. E. Garton 10380* (CAN, HAM, UC); Thunder Bay Dist., NW corner of Black Sturgeon Lake, *C. E. Garton 12208* (CAN, H, NDA, TRT, UBC); Thunder Bay Dist., SE corner of Black Sturgeon Lake, *C. E. Garton 12351* (CAN, DAO, TRT, UBC); Algoma Dist., 0.5 mi. N of Wawa along hwy 101, *C. E. Garton et al. 14320* (ACAD, CAN, H, MICH, NDA, NLU, SASK, TRT); Algoma Dist., mouth of Michipicoten R., *C. E. Garton et al. 14492* (ACAD, CAN, H, MICH, NDA, NLU, SASK, TRT, UBC); Pukaskwa National Park, 2.5 km E of Oiseau Bay, *C. E. Garton 16255* (CAN); 1 mi. N of Amherstview, *A. E. Garwood 1018* (TRT); Northumberland Co., Brighton Twp, Presque Isle Park, *J. Gillett & J. Calder 6337* (DAO, NY, TRT); Hastings Co., 3.5 mi. NNW of Marmora, *J. Gillett & J. Calder 6377* (DAO); Stormont Co., 3 mi. W of Cornwall, *J. Gillett & W. Dore 7639* (DAO); Stormont Co., Osnabruck Twp, 2 mi. NE of Wales, *J. Gillett 7794* (DAO); Renfrew Co., 2 mi. NE of Eganville, Mink Lake, *J. Gillett 9501* (DAO); Glengarry Co., Summerstown, *G. Gogo 470* (DAO); Algoma Dist., S Lizard Island, *C. O. Grassl 588* (MICH); Algoma Dist., Goulais Bay, *C. O. Grassl 590* (MICH); Algoma Dist., Leach Island, *C. O. Grassl 591* (MICH); Algoma Dist., Nestorville, *C. O. Grassl 5483* (MICH); Manitoulin Dist., Indian Village at South Bay, *C. O. Grassl 6004* (MICH); Manitoulin Dist., Little Current, *C. O. Grassl 6006* (MICH); Durham Co., 3 mi. NE of Blackstock, *E. Haber 82* (CAN); Durham Co., Cartwright Twp, 3 mi. NE of Blackstock, *E. Haber 538* (CAN, DAO, MTMG, TRT); York Co., Toronto, Serena Gundy Park, *E. Haber 541* (CAN, TRT); Ontario Co., Greenwood, Swiss Chalet Park, *E. Haber 548* (CAN, DAO, MTMG, TRT); York Co., Markham Twp, just E of Gormley, *E. Haber 551* (CAN, DAO, TRT); York Co., King Twp, ca. 2 mi. NW of Nobleton, *E. Haber 555* (CAN, DAO, MTMG, TRT); Midland, Wye Lake, *D. Haddow 126* (DAO); Frontenac Co., Bedford Twp, Frontenac Park, *R. Hainault & I. Macdonald 5132* (CAN, SASK); Peel Co., Cold Creek Swamp near Bolton, *J. M. Hamley in 1959* (TRT); Ottawa Dist., Carleton Co., Gloucester Twp, *E. Hart 1945* (UTC); Thunder Bay Dist., Fallingsnow Lake, *W. & M. Hartley 2116* (CAN, MAK, V); Hastings Co., 1 mi. W of Coe Hill, *C. Heidenreich 428* (DAO, TRT); Nipissing Dist., Notman Twp, *R. C. Hosie 118* (TRT); Thunder Bay Dist., Copper Island, *R. C. Hosie et al. 1708* (TRT, UC, WS); Thunder Bay Dist., Jackfish, *R. C. Hosie et al. 1710* (GH, MT, TRT); Thunder Bay Dist., Mortimer Island, *R. C. Hosie et al. 1711* (CAN, TRT); Algoma Dist., Magpie Falls, *R. C. Hosie et al. 1904* (HAM, TRT, UTC); Algoma Dist., vicinity of Michipicoten Harbour, *R. C. Hosie et al. 1905* (ACAD, NY, TRT); Algoma Dist., Mission

Lake Portage, *R. C. Hosie et al. 1906* (MIN, TRT); Haliburton Co., Harcourt Twp, *D. Hoy in 1974* (TRT); Ontario Co., Reach Twp, *D. Hoy et al. in 1975* (TRT); York Co., E Guillimbury Twp, *D. Joy et al. in 1977* (TRT); Chalk R., Dominion Forest Experiment Station, *I. Husitch in 1946* (CAN); Thunder Bay Dist., Cloud Bay, *D. L. Jacobs 22* (MIN); Smoke Lake, Algonquin Park, *M. F. Jackson in 1946* (TRT); Waterloo Co., Bridgeport Dam, *E. L. James 262* (HAM); Elgin Co., Malahide Twp, *L. James in 1950* (DAO); Elgin Co., 5 mi. SW of Aylmer, *L. James 1792* (DAO, PAC); Carleton Co., Ottawa, Dow's Swamp, *L. Jenkins 6594* (DAO); head of Surprize Lake, Thunder Cape, Lake Superior, *O. E. Jennings et al. 1943* (CM, CU, DAO); Rossport, *O. E. & G. K. Jennings 2724* (CM); along Kaministiquia R. near Stanley, *O. E. & G. K. Jennings 3132* (CM); Edwards Island, Lake Superior, *O. E. & G. K. Jennings 3761* (CM); SE corner Lake Nipigon, N of Orient, *O. E. & G. K. Jennings 6407* (CMI); 0.5 mi. W of Jellicoe, *O. E. & G. K. Jennings 14537* (CM); Oscar to Knowlton, *O. E. & G. K. Jennings 15536* (DAO); Niagra Glen, *F. Johnson in 1925* (NY); ca. 10 mi. N of Finland, *J. Kane 2127* (WIS); Glencoe, *N. Keith in 1893* (MTMG); Kenora Dist., Rushing R. W of hwy 71, 4 mi. S of hwy 17, *G. M. Keleher 127* (WIN); Rainy River Dist., Basswood Lake near Ottawa Island, *D. Knight 200* (AUG); Frontenac Co., Eagle Lake, *P. V. Krokov in 1939* (TRT); Temagami Forest Reserve, Bear Island, *P. V. Krotkov 5477* (TRT); Bruce Peninsula, Tobermory, *P. V. Krotkov 7635* (GH, TRT); Bruce Peninsula, Stokes Bay, *P. V. Krotkov 9242* (CU, TRT, US, WIS); Bruce Peninsula, Hope Bay, *P. V. Krotkov 9858* (TRT); Bruce Peninsula, Dryers Bay, *P. V. Krotkov 10731* (DAO, TRT); Baswood Lake, Bayley Bay, *O. Lakela et al. 16339* (MIN); Norfolk Co., Windham Twp, *M. Landon 492* (HAM); Norfolk Co., Turkey Point, *M. Landon 493* (TRT); Portage, Long Lake, *E. E. Laughlin 1353* (OS); Sand R. at Lake Superior, *M. Lechowitz & W. Post, III in 1973* (WIS); Spike Lake on rte 556, NE of Sault Ste. Marie, *M. Lechowitz & W. Post, III in 1973* (WIS); Newington, *J. H. Lemon 817* (UBC); Waterloo Co., Preston, *R. M. Lewis 153* (TRT); Golden Lake, *H. Lloyd in 1948* (DAO); St. Lanark Co., S of Bolingbroke, *R. A. Lubue 783* (TRT); near Belleville, *J. Macoun in 1865* (CAN); Hastings Co., *J. Macoun 58* (GH); near Brittania, *J. Macoun 567* (DAO); Tilsonburg, *J. Macoun 44423* (CAN, GH); Mississauga, Rattray Marsh, *I. Macdonald 1598* (CAN); Peel Co., Brampton, *H. G. Macklin in 1935* (HAM); Norfolk Co., 5 mi. NE of Port Rowan, *P. F. Maycock 1702* (MTMG); Huron Co., 2 mi. NE of Bayfield, *P. F. Maycock & O. Maryniak 2843* (MTMG); Huron Co., Tuckersmith Twp, 3 mi. NE of Hensall, *P. F. Maycock 2873* (MTMG); Elgin Co., 2.5 mi. NW of Wallacetown, *P. F. Maycock 5246* (MTMG); Norfolk Co., 2 mi. N of Middleton, *P. F. Maycock & O. Maryniak 6224* (DAO, MTMG); Norfolk Co., 3 mi. N of Port Dover, *P. F. Maycock & E. Visser 7961* (MTMG, NCU, TRT); Lincoln Co., Glen Elgin, *W. McCalla in 1896* (ALTA); Muskaka Co., MacTier, *E. H. McClelland in 1921* (CM); 60 mi. SSE of Red Lake, near Cedar Lake, *D. McMillan 60* (DAO); Algoma Dist., Michipicoten near Wawa, *J. McNeill 3010* (DAO); Cochrane Dist., SW of Kapuskasing in Sulman Twp, *J. B. Millar & E. Bonner 61* (TRT); Louth Twp, 1 mi. S of Jordan, *B. Miller 398* (HAM); Welland Co., Stamford Twp, Niagara Gorge, *B. Miller 446* (HAM); Merivale, *W. Minshall in 1933* (DAO); Carleton Co., Fitzroy Twp, *W. Minshall 3302* (DAO); Brant Co., Brantford Twp, *W. Minshall 3904* (DAO); Sandborn Bay, vicinity of Sandy Lake, *D. R. Moir 4099* (GH, MIN, NDA); Waterloo Co., Waterloo, *F. Montgomery 262* (DAO, GH); Deep River, *M. I. Moore in 1966* (KYO); Glen Morris to Wrigley's Corner, *J. K. Morton NA 3089* (CAN); Parry Sound Dist., Laurier, *L. R. Moyer 2611* (MIN, NY); Georgian Bay National Park, *R. Muir 62B106* (DAO); Renfrew Co., Maria Twp, 0.75 mi. W of Bissett, *G. Mulligan 598* (DAO); Kent Co., Rondeau Park, *R. W. Neal 359* (HAM); Thunder Bay Dist., Sauerbrei Lake, *A. Oaks 1098* (TRT); Russell Co., 0.4 mi. W of Cumberland, *J. Op de Beeck in 1969* (MTMG); Lanarck Co., ca. 5.5 mi. S of Perth, *A. Pokorny in 1968* (MTMG); Hudson Bay Lowlands, Attawapiskat R. near junction with Muketei R., *A. E. Porsild et al. 20178* (CAN); Niagara Falls, *W. J. Potter in 1907* (TRT); Thunder Bay Dist., Paipoonge Twp, *J. Purchase in 1960* (DAO, TRT); Algoma Dist., ca. 1.7 mi. N of Fenwick Twp school, *J. Purchase in 1960* (DAO, TRT); Algoma Dist., Lake Superior Provincial Park, *J. Purchase in 1961* (TRT); Speed R., Guelph, *H. N. Racicot in 1921* (HAM); Simcoe Co., Nottawasaga Twp, *A. A. Reznicek 3208* (TRT); Cochrane Dist., Dyer Twp, Onakawana, *J. L. Riley in 1972* (TRT); Cochrane Dist., Pierre–Montreuil Park Reserve, *J. L. Riley in 1974* (TRT); Rainy River Dist., 1.5 km NE of Atikokan, *G. S. Ringius 15* (AKAD); York Co., Scarborough Twp, *W. Robbins in 1908* (DAO); 7 mi. W of Chapleau, *D. Ropke 304* (DAO); Charleton Co., Gloucester Twp, *H. Senn 1918* (DAO); Hastings Co., Modoc Twp, 1.5 mi. N of Cooper, *M. J. Shchepanek & J. H. Soper 594* (CAN, MTMG, SASK, TRT, WTU); Perth Co., Fullerton Twp, 3 mi. SE of Mitchell, *J. K. Shields 223* (CAN, TRT); Haliburton Co., Minden Twp, *E. & E. Skelton 337* (TRT); Muskoka Dist., near Huntsville, *J. H. Soper in 1949* (TRT); Norfolk Co., Lake Erie, Turkey Point, *J. H. Soper 175* (DAO); Carleton Co., Goulbourn Twp, *J. H. Soper et al. 3224* (DAO, TRT); Durham Co., Hope Twp, 5 mi. W of Port Hope, *J. H. Soper & H. Dale 4007* (DAO, TRT); Brant Co., Dumfries Twp, 2 mi. E of Ayr, *J. H. Soper & H. Dale 4123* (DAO, GH, TRT); York Co., Vaughan Twp, 3 mi. E of Kleinburg, *J. H. Soper & H. Dale 4131* (DAO, GH, TRT); Simcoe Co., Adlaja Twp, ca. 3 mi. NE of Hockley, *J. H. Soper & J. K. Shields 4827* (TRT); Simcoe Co., Nottawasaga Twp, *J. H. Soper & J. K. Shields 4834* (CAN, MT, NCU, TRT); Parry Sound Dist., Croft Twp, *J. H. Soper 5312* (MTMG, TRT); Leeds Co., near

Chaffey's Locks, Lake Opinicon, *J. H. Soper 5579* (ACAD, TRT); Huron Co., ca. 8.5 mi. E of Brussels, *J. H. Soper & G. Fleischmann 6412* (CAN, TRT); Grey Co., Osprey Twp, *J. H. Soper et al. 7475* (CAN, MIN, TRT); Manitoulin Dist., Frechette Bay just W of Murphy Point, *J. H. Soper & C. Heidenreich 8985* (CAN, DAO, TRT); Manitoulin Dist., Heywood Island, *J. H. Soper & W. D. Murray 10070* (CAN, NCU, TRT); Thunder Bay Dist., Michipicoten Island, *J. H. Soper & F. A. Fraser 10939* (CAN, TRT); Christina, *G. Stirrett & D. Arnott in 1936* (DAO); Wellington Co., Puslinch, *J. J. Stroud in 1937* (TRT); Middlesex Co., London Twp, *W. D. Sutton 151* (TRT); Tillsonburg, *A. Tamsalu in 1956* (HAM); Simcoe Co., Dunedin, *T. M. C. Taylor in 1934* (TRT); Thunder Bay Dist., Norma Creek, *T. M. C. Taylor 736* (GH); Thunder Bay Dist., Red Sandstone Lake, *T. M. C. Taylor 826* (DS, TRT, UC, UTC); Thunder Bay Dist., Michipicoten Island, *J. H. Soper & F. A. Fraser 10939* (CAN, TRT); Christina, *G. Stirrett & D. Arnott in 1936* (DAO); Wellington Co., Puslinch, *J. J. Stroud in 1937* (TRT); Middlesex Co., London Twp, *W. D. Sutton 151* (TRT); Tillsonburg, *A. tamsalu in 1956* (HAM); Simcoe Co., Dunedin, *T. M. C. Taylor in 1934* (TRT); Thunder Bay Dist., Norma Creek, *T. M. C. Taylor 736* (GH); Thunder Bay Dist., Red Sandstone Lake, *T. M. C. Taylor 826* (DS, TRT, UC, UTC); Thunder Bay Dist., Port Coldwell, *T. M. C. Taylor et al. 1208* (CAN, TRT, UBC); Thunder Bay Dist., Heron Bay, *T. M. C. Taylor et al. 1210* (CAN, TRT, UBC); Algoma Dist., Batchawana Island, *T. M. C. Taylor et al. 1866* (TRT, V); Algoma Dist., Havilland Bay, *T. M. C. Taylor et al. 1867* (MT, TRT); Algoma Dist., Mamainse Point, *T. M. C. Taylor et al. 1868* (CAN, TRT, UBC, WTU); Algoma Dist., Coppermine Point, *T. M. C. Taylor et al. 2412* (TRT, UTC); Perth Co., Wallace Twp, *G. R. Thaler 226* (TRT); Huron Co., Morris Twp, Burssels, *G. R. Thaler 262* (TRT); Huron Co., Wawanosh Twp, Wingham, *G. R. Thaler 269* (TRT); Perth Co., Hibbert Twp, Staffa, *G. R. Thaler 272* (TRT); Dufferin Co., Mono Twp, Orangeville, *G. R. Thaler 278* (TRT); Middlesex Co., Lobo Twp, *G. R. Thaler 288* (TRT); Waterloo Co., Wilmot Twp, New Hamburg, *G. R. Thaler 292* (TRT); Huron Co., Turnberry Twp, Wroxter, *G. R. Thaler 395* (TRT); Huron Co., Hullett Twp, Londesborough, *G. R. Thaler 417* (TRT); Perth Co., Logan Twp, Mitchell, *G. R. Thaler 433* (TRT); Algoma Dist., Sand R. near its mouth, Lake Superior, *E. G. Voss & R. L. Jeanne 10613* (TRT); Simcoe Co., De Grassi Point, Lake Simcoe, *E. Walker in 1894* (TRT); York Co., King Twp, *E. Walshe 129* (CAN, DAO, MTMG, TRT); Bruce Peninsula, Red Bay, *W. R. Watson 3255* (TRT); Algonquin Park, Joe Lake, *W. R. Watson 3795* (DAO); Algonquin Park, N side of Island Lake, *W. R. Watson 4281* (ACAD, TRT); Edmonton, *J. White, 9066* (CAN); Muskoka Co., Morrison Twp, *R. E. Whiting 781* (TRT); vicinity of Fort William, *C. Williamson 1822* (PH); Bryon Region, *A. Wood in 1934* (DAO); Elgin Co., Yarmouth Twp, *D. Young 119* (TRT). PRINCE EDWARD ISLAND: Kings Co., Bay Fortune, *H. E. Aitken 42* (ACAD); Prince Co., Campbellton, *D. Erskine & A. J. Smith 1926A* (DAO); Kings Co., Bear R., ca. 1 mi. W of station, *D. Erskine & A. J. Smith 1991* (ACAD, DAO, MT); Queens Co., Charlottetown, *M. L. Fernald et al. 7838* (PH); Kings Co., Murray R., *D. Griffin in 1970* (TUR); Tracadie, *J. Macoun 9067* (CAN); Bideford, *A. R. A. Taylor in 1948* (DAO, UNB). QUEBEC: Saguenay Co., Natashquan, *E. C. Abbe 1252* (GH, MIN); Gaspe-Est Co., Perce, *J. Adams in 1935* (DAO); Gatineau Co., Blue Sea Lake, *C. Anderson in 1945* (CAN); Gatineau Co., above Kirk's Ferry, *C. Anderson in 1946* (CAN); Gatineau Co., Chilcott's Bog near Alcove, *C. Anderson in 1952* (CAN); Brome Co., Abercorn, *P. Bahr in 1963* (MTMG); Compton Co., Birchton P.O., *J. A. Bailey 1557* (TRT, V); West Abitibi Co., La Sarre, 14 mi. W at Lake Abitibi, *W. K. W. Baldwin & A. J. Breitung 2869* (CAN, GH, MT); Abitibi Co., Taschereau, *W. K. W. Baldwin & A. J. Breitung 5243* (CAN, MT, MTMG); Timiskaming Co., Ville Marie, 3 mi. S at Baie Laperriere, *W. K. W. Baldwin 5942* (CAN, MT); Gaspe-Est Co., Grande-Riviere, *R. Barabe & E. Campagna in 1940* (DAO); Bonaventure Co., Port-Daniel, *R. Barabe & L. Dube in 1940* (DAO); Lac St. Jean-Ouest Co., Roberval, *J. Barnhart 732* (NY); Rimouski Co., Bic, *E. Bartram & B. Long 231* (PH); Rouville Co., Mt. St.-Hilaire, *A. Beaulieu in 1962* (MTMG); Stanstead Co., Beebe, *A. Beaulieu 16* (DAO, MTMG); Matapedia Co., Amqui, *A. Belzile & C. Gervais 28624* (DAO, UBC); Magdalen Islands, Amherst Island, S Cape, *P. A. Bentley & D. H. Webster 364* (DAO); Riviere du Loup Co., Riviere du Loup, *A. Blain et al. in 1941* (MT); Matapedia Co., Sainte-Irene, *A. Blain 184* (CAN, GH, MT, US); Richmond Co., between Burbank Hill & Shipton Pinnacle, *V. Blais & C. Hamel 11197* (ACAD, CM, SASK, TRT); Richmond Co., Richmond, *J. Blankenship in 1897* (GH); Terrebonne Co., Lac Tremblant, *C. M. Boardman 138* (CM); Matane Co., Mont Blanc, *B. Boivin & A. Blain 536* (MT); Matane Co., mt. to the E of Matane, *B. Boivin & A. Blain 584* (DAO, ISC, MT); Charlevoix Co., Les Eboulements, *B. Boivin 1419* (CU, DAO, ISC, MT, TEX); Huntingdon Co., St.-Amicet, *A. Bouchard & S. Hay 4215* (CAN); Megantic Co., St. Ferdinand ("Bernierville"), *A. Bouchard et al. 69-652* (MTMG); Frontenac Co., 1.7 mi. N of St.-Cecile, *A. Bouchard & H. Gilbey 69-656* (MTMG); Sherbrooke Co., 2 mi. N of Coaticook, *A. Bouchard & D. Gilbey 69-657* (MTMG); Lac St.-Jean Est Co., Chambord, *C. Bouchard 70-566* (DAO, MAK); Lac St.-Jean Est Co., Hebertville, *C. Bouchard 70-676* (DAO); Saguenay Co., Ilets Jeremie, *S. Brisson 889* (MT); Chicoutimi Co., Anse St. Jean, *S. Brisson 5642* (MT); Chicoutimi Co., Petit Saguenay, *S. Brisson 5739* (MT); Chicoutimi Co., Cap a l'Est, *S. Brisson 5774* (MT); Gaspe Ouest Co., Courcelette, Plaque-Malade, *S. Brisson et al. 6133* (CAN); Saguenay Co., Grandes Bergeronnes, *S. Brisson 60-280* (MT); Chicoutimi Co., Harvey, Cap

Jaseux, *S. Brisson 74189* (CAN, VSC); *S. Brisson 76521* (MTMG, NLU); Bonaventure Co., Cascapedia Valley, *J.-D. Brule et al. 35130* (MT); Saguenay Co., Blanc-Sablon, *J. Brunel 108* (MT); Montcalm Co., Provost Lake, St. Donat, *M. Cailloux in 1936* (MT); Papineau Co., Templeton Parish, *J. Calder M-83* (DAO); L'Islet Co., Trois-Saumons, *J. Cayouette 1045* (H); Matane Co., St.-Rene Goupil, *R. & J. Cayouette 55-44* (TRT); Matane Co., St.-Nil, *R. Cayouette 56-282* (H); Chicoutimi Co., St.-Fulgence, *R. Cayouette 58-117* (DAO); Chicoutimi Co., Labrousse, *R. Cayouette & S. Brisson 64717* (CAN, DAO, MT, SASK); Richmond Co., Cleveland, *E. Chamberlain & C. Knowlton in 1923* (GH); Missisquoi Co., Georgeville, *J. R. Churchill in 1902* (GH, MT); Rouville Co., Rougemont, *L. Cinq-Mars in 1951* (DAO, MT, MTJB); Bonaventure Co., Matapedia, *L. Cinq-Mars L-279* (DAO); Charlevoix Co., Notre Dame des Monts, *L. Cinq-Mars et al. 66-325* (ACAD, DAO, GH, MAK, MTMG, OSC, TRT, UBC, UC, UNB, V); Missisquoi Co., Frelighsburgh, *L. Cinq-Mars & A. Vezina 67-85* (ACAD, CAN, DAO, MAK, MTMG, OSC, TRT, UBC, UC, V); L'Islet Co., Trois-Saumons, *L. Cinq-Mars & P. Masson 71-373* (TRT); Matane Co., W of Grosses Roches, *R. T. Clausen & H. Trapido 2861* (BH, CU, PAC); Papineau Co., Buckingham, *Fr. Cleonique 7097* (MT); Montreal & Jesus Islands Co., Mont-Royal, *Fr. Cleonique 9213* (MT); Deaux-Montagnes Co., Okla, *Fr. Cleonique 11447* (MT); Joliette Co., Ste.-Beatrix, *L. P. Coiteux 98* (MT); Gaspe-Est Co., mouth of Dartmouth R., *J. Collins et al. 5123* (GH); Gaspe-Ouest Co., Cap Au Renard, *W. P. Cottam 11678* (UT); Montmorency Co., Laurentides Park, Lake Horatio-Walker, *Y. Desmarais 301* (MT, WIS); Gatineau Co., Hincko Twp, *W. G. Dore & F. Beales 22359* (DAO, MTMG, TRT); Deaux-Montagnes Co., Oka, Sulpiciens, *A. Dubois 427* (NY); Matane Co., 3 mi. W of Metis Beach, *G. & P. DuBoulay 3225* (MTMG); Arthabaska Co., Trois Lacs, *Fr. Euplius 537* (MT); Shefford Co., Granby, *Fr. Fabius 367* (CAN, MT); Gaspe-Ouest Co., Mt. St.-Anne, *FF. Fabius & Allyre 3088* (DAO); Rouville Co., Mont Yamaska, *Fr. Fabius 5525* (DAO); Gatineau Co., Blue Sea Lake, Big Island, *N. C. Fassett 18087* (WIS); Magdalen Islands, Grindstone Island, Grindstone, *M. L. Fernald et al. 7836* (CAN, GH, MT, NY, PH, WS); Magdalen Island, E Cape & E Point, *M. L. Fernald et al. 7837* (PH); Kamouraska Co., Ste. Anne, *F. F. Forbes in 1907* (DS); Matane Co., Little Metis, *J. Fowler in 1906* (GH, TRT), *J. Fowler in 1908* (MO); Gatineau Co., Hull, *F. Fyles in 1911* (DAO); Quebec Co., Montmorency Falls, *F. Fyles in 1915* (DAO); Gatineau Co., Gatineau Park, *J. M. Gillett 15177* (CAN, TRT); Bonaventure Co., Bonaventure R., *V. Gerardin et al. 5211* (DAO); Madeleine Isle Co., Grosse Island, Rockhill Point, *M. Grandtner et al. 8255* (DAO); Montmorency Co., Boischatel, *M. Gravel et al. 69-116* (ACAD, MTMG, OS, PH, TRT, UBC, UNB); Terrebonne Co., Lac L'Achigan, near Shawbridge, *P. S. Green in 1959* (UC); Wolfe Co., Lake Nicolet, Gartby, *C. Hamel 11537* (CAN, COLO, MTMG, UBC); Wolfe Co., Lake Aylmer, Garthby, *C. Hamel 12569* (COLO, MTMG); Wolfe Co., Lake Elgin, Stratford, *C. Hamel 14585* (BALT, H); Wolfe Co., Weedon, *C. Hamel 14783* (CAN, CM, DAO); Wolfe Co., St.-Adrien de Ham, *C. Hamel 18355* (ACAD, TRT, UC); Lac St. Jean Ouest Co., Peribonka Dist., Lac Alex, *I. Husitch 282* (CAN, H); Abitibi Co., 24 mi. S of Val d'Or, *I. Husitch 403* (MTJB); L'Islet Co., *H. A. C. Jackson 99* (DAO, KANU); Gatineau Co., W of Kazabazua, *L. Jenkins et al. 3639* (DAO); Argenteuil Co., Greenville Twp, *L. Jenkins 9065* (DAO); Magdalen Islands, Grindstone Island, *F. Johansen in 1917* (CAN); Magdalen Islands, Amherst, *F. Johansen in 1917* (CAN); Brome Co., Bolton, *A. Johnstone in 1963* (MTMG); Missisquoi Co., Phillipsburg, *C. Knowlton in 1923* (GH); Temiscouata Co., Caban, *J. Kucyniak & D. Tardif 286* (MT); Labelle Co., Nominique, *P. Labarre in 1936* (DAO); St. Maurice Co., La Maurice National Park, *G. Lamoureaux & L. Durand 71-42-12* (CAN); Missisquoi Co., Phillipsburg, *C. Lanouette in 1936* (MT); Missisquoi Co., 70 mi. SE of Montreal, Lake Selby, *G. F. Ledingham 1670* (USAS); Riviere du Loup Co., St. Francoise, *E. Lepage 15383* (DAO); Rimouski Co., St.-Fabien-sur-Mer, *E. Lepage 15841* (DAO, SASK); Riviere du Loup Co., Trois Pistoles, *E. Lepage 16961* (DAO); Saguenay Co., St. Mary Islands, Cliff Island, *H. F. Lewis in 1927* (CAN, CU); Saguenay Co., Natashquan, *H. F. Lewis in 1927* (CAN, CU); Saguenay Co., Tabatiere, *H. F. Lewis in 1928* (CAN, CU); Deaux-Montagnes Co., La Trappe, Ile Bizard, *P. Louis-Marie in 1933* (SMU); Labelle Co., Bellerive, *FF. Lucien & Eloi 678* (GH, MT); Anticosti Island, Salt Lake, *J. Macoun 817* (US); Quebec Co., Montmorency Falls, *J. Macoun 67942* (CAN, GH); Gatineau Co., Farrellton, *M. O. Malte 262/23* (CAN, TRT); Gatineau Co., Wakefield, *M. O. Malte 388/22* (CAN, MIN, W); Gaspe-Est Co., Bonaventure Island, *W. Manger 51* (DAO); Lac St. Jean Ouest Co., St. Felicien, *Br. Marie-Anselm 70* (DAO); Labelle Co. 15 mi. N of Mont Laurier, *F. Marie-Victorin et al. 214* (GH, MT); Portneuf Co., Petit Saguenay, *F. Marie-Victorin 10800* (MT); Madeleine Islands, Bassin Island, *FF. Marie-Victorin & Rolland-Germain 10801* (DAO, GH, MIN, MT, US, WS); Terrebonne Co., vicinity of St. Jerome, *FF. Marie-Victorin 11271* (GH, MT, US, WS); Anticosti Island, Riviere des Caps, *FF. Marie-Victorin & Rolland-Germain 27229* (CAS, GH, MT); Saguenay Co., Natashquan, *FF. Marie-Victorin & Rolland-Germain 28111* (MT); Brome Co., Bolton Pass, *F. Marie-Victorin et al. 56294* (MT); Wolfe Co., Weedon, *P. Masson 12490* (MTMG); Campton Co., Ste.-Marguerite-de-Linwick, *P. Masson 13329* (TRT); Rouville Co., Mont St. Hilaire, *P. Maycock & O. Maryniak 3255* (CAN, DAO, MTMG, TRT); Argenteuil Co., 4 mi. NW of Lachute, *P. Maycock & R. Goodland 9164* (MTMG); Brome Co., 2 mi. E of Sweetsburg, *P. Maycock et al. 11759* (MTMG); Brome Co., ca. 2 mi. E of Knowlton, *P. Maycock et al. 11760*

(MTMG); Frontenac Co., Mont Gosfors, *P. Maycock & A. Bouchard 12796* (MTMG); Megantic Co. (Richmond Co.?), Asbestos, *R. Meilleur 1022* (MTJB); Missisquoi Co., Philipsburg, *R. Meilleur 1417* (MTJB); Portneuf Co., St. Augustin Lake, *Fr. Michel 250* (MT); Portneuf Co., St. Raymond, *Fr. Michel 1550* (MT); Quebec Co., Charlesbourg, *Fr. Michel 2078* (MT); Gaspe-Est Co., Perce, *J. Mignault in 1929* (MT); Saguenay Co., Les Escoumains, *C. Morin 862* (MT); Vaudreuil Co., Mt. Rigaud, *L. Newstrom 722B* (MTMG); Berthier Co., just S of Berthierville, *J. Op de Beeck & L. Gohier in 1969* (MTMG); Kamouraska Co., Lake Disparu, 31 mi. from St.-Anne, *R. Paquin & A. Payette 178* (DAO); Matane Co., S end of Matane Lake, *J. H. Pierce & W. H. Hodge in 1934* (TRT); L'Islet Co., Trois Saumon Lake, *J. Perras 71-202* (CAN); Gaspe-Est Co., Chandler, *T. Proulx in 1933* (MTMG, OSC, UBC, UC, UNB); Bonaventure Co., Grand Cascapedia, *C. Riley in 1934* (NY, WIS); Vaudreuil Co., Rigaud, *A. Robert 656* (MT); Montcalm Co., Mont Tremblant Park, Rolland, *Fr. Rolland-Germain 334* (DAO, MT); Montcalm Co., Mont Tremblant, *Fr. Rolland-Germain 539* (CAN); Argenteuil Co., St. Adolphe, *Fr. Rolland-Germain 7574* (ACAD, CAN, DAO, FSU, GH, MIN, MT, NY, TRT, UC, US); Terrebonne Co., St.-Hippolyte, *Fr. Rolland-Germain 30207* (MT); Argenteuil Co., St.-Adolphe d'Howard, *Fr. Rolland-Germain 36333* (DAO); Gaspe-Ouest Co., several mi. W of Mont St. Pierre, *G. B. Rossbach 4453* (WVW); Gaspe-Ouest Co., SE of Ste. Anne des Monts, *G. B. Rossbach 4454* (WVW); Terrebonne Co., Lake Mercier, *E. Rouleau 2184* (MT); Terrebonne Co., Val David, *E. Rouleau 2190* (MT); Portneuf Co., St. Augustin, *C. Rosseau & S. Payette in 1964* (UBC); Mistasini Terr., Chute-Cachee Bay, Dauphin Peninsula, *J. Rousseau & E. Rouleau 1087* (B, CAN, GH, MT, NY); Rimouski Co., Bic, *J. Rousseau 24916* (MT); Rimouski Co., Cap Errage, *J. Rousseau 26502* (CAS, DAO, MT); Rimouski Co., Cap a L'Original, *J. Rousseau 26734* (GH, MT, WS); Gaspe-Ouest Co., Mont Louis, *J. Rousseau 31138* (DAO, GH, MT); Bonaventure Co., junction of Restigouche & Matapedia Rivers, *J. Rousseau 32245* (GH); Anticosti Island, Riviere a la Chute, *J. Rousseau 52398* (MT); Labelle Co., Nominique, *Fr. E. Roy 2270* (MT); Saguenay Co., Tabatiere, Boishebert, *H. St. John 90614* (CAN); Saguenay Co., Brouague, Petit R. Coxipi, *H. St. John 90615* (CAN, GH); Bonaventure Co., Bonaventure, *Fr. Samuel 49* (MT); Madeleine Islands, Ile aux Meules, *Fr. Samuel 5018* (MT); Madeleine Islands, Il Havre aux Maisons, *Fr. Samuels 5352* (MT); Gatineau Co., Aylmer, *H. S. Saunders 99* (TRT); Argenteuil Co., Morin Heights, *H. Scoggan 180* (CAN); Gatineau Co., Masham Twp, Johnston, *H. Senn et al. 109* (DAO); Pontiac Co., Lochaber Parish, 2 mi. N of Silver Creek, *H. Senn & M. Zinck 504* (DAO, MO); Gatineau Co., Gatineau Park, Eardley Parish, *H. Senn & M. Zinck 646* (DAO); Pontiac Co., Aldfield Parish, *H. Senn et al. 680* (DAO); Gatineau Co., Wakefield Parish, 4 mi. E of Wakefield, *H. Senn et al. 851* (DAO); Gatineau Co., B'Ake Twp, 3 mi. E of Point Comfort, *M. Shchepanek & A. Dugal 935* (CAN); Papineau Co., Portland W Twp, 3 mi. NE of Poltimore, *M. J. Shchepanek & A. Dugal 982* (CAN); St.-Maurice Co., Pointe-du-Lac, *F. Stanislas 565* (MT); Terrebonne Co., Lake Carre, *D. Swales 5271* (MTMG); Gaspe-Ouest Co., Marsoui, *H. W. Swift in 1958* (DAO); Matane Co., ca. 1 mi. inland from river near Grosses Roches, *H. W. Swift in 1958* (DAO); Gaspe-Est Co., Dartmouth R., *B. Tache & A. Lepage 253* (MT); Berthier Co., Lavaltrie, *L. M. Terrill 902* (MTMG); Gaspe-Ouest Co., Mont St. Pierre, *L. Terrill 2124* (CAN); Gaspe-Est Co., Bonaventure Island, *L. Terrill 3229* (CAN); Temiscouata Co., Tobin, *L. Terrill 5305* (CAN); Rouville Co., Yamaska Mt., *A. Walther in 1962* (MTMG); Rouville Co., Rougemont Mt., *A. Walther & A. Auclair in 1962* (MTMG); Brome Co., Brome Mt., Spruce Peak, *A. Walther & A. Auclair in 1962* (MTMG); Magdeleine Islands, Amherst Island, S Cape, *D. H. Webster & P. A. Bentley 364* (ACAD); Matane Co., W of St. Edward de Mechins, *K. M. & M. C. Wiegand 239* (CU); Bonaventure Co., New Carlisle, *E. Williams & M. L. Fernald in 1902* (GH); Deaux-Montagnes Co., St. Scholastique, *R. Wishart in 1971* (MTMG); Stanstead Co., Hatley, *without collector 9381* (GH); Sherbrooke Co., Ascot, *without collector in 1850* (MTMG). SASKATCHEWAN: Big Sandy Lake, NW end of Lake, *G. W. Argus & J. H. Hudson 4466* (DAO); S end of Candle Lake, just N of Hayes Beach, *G. W. Argus 4921* (DAO, RM); McKague, *A. J. Breitung in 1934* (DAO); N of Churchill R., near Windrum Lake, *W. Bryenton 149* (CAN); Waskesiu Park, Waskesiu Narrows, *R. Connel in 1960* (SASK); White Fox, *G. E. Fraser in 1950* (SASK); Prince Albert National Park, Lake Waskesiu, *W. P. Fraser in 1930* (SASK); Turtle Lake, *W. P. Fraser in 1932* (SASK); Mistatim, *W. Haliday 123* (CAN); Hidden Bay of Wolaston Lake, *V. L. Harms 21595* (SASK); Saskatoon Dist., Sutherland, *J. H. Hudson 2183* (DAO); vicinity of Wood Mt. Post, *J. H. Hudson 2352* (COLO, DAO, SASK); Perdue, *J. H. Hudson 3432* (USAS); Candle Lake Region, Candle Lake Road, *J. K. Jeglum 689-62B* (SASK); Saskatoon Dist., W side of Pike Lake, SW of Saskatoon, *L. Jenkins et al. 1277* (DAO); S of Cherry Lake, 11 mi SE of Indian Head, *G. J. Jones & G. F. Ledingham 738* (DAO, USAS); Sunny Brow, *I. Laycock s.n.* (DAO); 12 mi. S of Indian Head, below Big Spring, Cherry Lake, *G. F. Ledingham et al. 147* (DAO, USAS); 3 mi. SW of Torch Lake, Candle Lake, *G. F. Ledingham & J. Hudson 2141* (SMU, USAS); 20 mi. N of Regina, *G. F. Ledingham et al. 5250* (USAS); Lac la Ronge, *G. F. Ledingham 48425* (SMU, USAS); Paradise Hill, *M. M. Price 55002* (DAO); E Bay, Dort Lake, *G. S. Riley 48/3* (DAO); Lake Washesiu, *E. G. & R. C. Russell in 1932* (TRT); Indian Head, *B. J. Sallans in 1936* (TRT); Madge Lake, *C. Shaw S-2761* (DAO); 0.4 mi. E of W gate to park at Madge Lake, *N. A. Skoglund 536* (SASK); ca. 2 mi. W of Southend, Numaloin

Bay of Reindeer Lake, *J. Ternier & S. Lamont 599* (SASK); mi. 1.25 N of La Ronge on hwy 102, *J. Ternier & M. Jasieniuk 2096* (SASK); ca. 235 mi. N of La Ronge, Geikie R., mi. 116, hwy 105, *J. Ternier & M. Jasieniuk 2547* (SASK); Qu'Appelle Valley Region, E of Tantallon, *B. deVries 274* (DAO). ST. PIERRE & MIQUELON: St. Pierre, Etang Du Milieu, *L. Arsene 319* (NY); St. Pierre, Savoyard, *Le Gallo 447* (MT); St. Pierre, Langlade, Miquelon, *M. Le Hors s.n.* (DAO).

UNITED STATES. ALASKA: near Valdez, mile 10, Richardson Hwy, *T. Ahti 23904* (H); Valdez Township, ca. 4 mi. from Valdez along Prince William Sound's shore, *B. Cumby 269* (WILLI); Keystone Canyon, Valdez Road, *Dutilly et al. 21408* (RSA); Juneau, *J. Anderson 6315* (CAN, DAO, GH, MTJB, NO, NY, PH, RM, TEX), *F. Coville & T. Kearney, Jr. 2524* (GH, US), *W. Trelease 4439* (MO); mile 28 on road N from Juneau to Auke Bay, *P. Hoch 1812* (KYO, MHA, MO); Juneau, upper Gold Creek Canyon, *M. Williams 1932* (ORE, OSC); Sitka, *H. Cowles 1315* (MO, US), *L. Smith 101* (ORE, OSC), *A. Eastwood 951* (CAS); *W. Evans 231* (US); near Fairbanks, *L. Jordal 3518* (BH, US); ca. 138 mi. N of Fairbanks, *E. Scamman 327* (GH, MASS, US); Kodiak, Sitkalidak Island, *W. Eyerdam 36* (CAS, DS, GH, NY, UC, US); Kodiak Island Three Saints Bay, *B. Nybakken 2810* (WIS); Kiliuda Bay, *E. Beals in 1961* (WIS), Three Saints Bay, *W. Eyerdam 607* (CAS, DS, NY), Old Harbour, *W. Eyerdam 703* (CAN, CAS, US); Kodiak Islands, Raspberry Island, Port Vita, *W. J. Eyerdam 3871* (CAS, DAO, UC, WS); Circle Hot Springs, *H. Shacklette 6421* (US); Hot Springs area at Circle Hot Springs, *J. Taylor 3292* (OKL, SMU); Herendeen Bay, *"Albatross" in 1890* (US); Skagway, *J. Anderson 847* (NY); Matanuska, *J. P. Anderson 1360* (CAN, POM); Seward, *L. Henderson 14893* (ORE), *L. I. & J. Grinnell 476* (CU); McDonald Lake, *J. Burcham 134* (US); Anchorage area, by Ship Creek, *C. York 326* (TEX); Hyder, *K. Whited 1289* (ND, UTC); Kenai Peninsula, Russian R. near junction with Kenai R., *S. L. Welsh & G. Moore 6018* (MIN, MISS, NY); Burrough's Bay, *Walker & Walker 1020* (CM, DS, GH, MO, RM, US); Prince of Wales Island, Klawak Lake, *Mr. & Mrs. E. P. Walker 1010* (CM, DS, GH, MO, NY, RM, US); Bell Island, Sulphur Springs, *Mr. & Mrs. E. P. Walker 953* (CM, DS, GH, MO, NY, RM, UC, US, WTU); Chichagoff Island, Ford Arm, *Mr. & Mrs. E. P. Walker 857* (CM, GH, MO, RM, US), *858* (DS, GH, MO, NY, RM, UC, WTU); Afognak Island, Discoverer Bay, *J. Taggart & C. Zabel 93* (UTC); Yakutat, *L. Stair in 1945* (PH); Admiralty Island, Hawk Inlet, *Mrs. F. M. Stephens in 1926* (CAS); 24 mi. SE of Whittier, Eshamy, *J. D. Solf 50* (WS, WTU); Kukak Bay, *Saunders 4443* (MO); Tanona R., Hot Springs, *A. & R. Porsild 656* (CAN, GH, US); Matanuska Valley, *L. Palmer 195* (NA); Bristol Bay District, Napnek, *I. L. Norberg in 1946* (SMU); Chichagof Island, Hoonah, *I. L. Norberg 247* (CAN, DS, GH, NY, US), Chignik, *I. L. Norberg in 1945* (CAN, GH); Glacier Bay National Monument, Muir Point, *M. G. Noble & C. D. Sandgren 400* (MIN); Yentna District, above Morgan Creek Flats, *R. V. Moran 66* (DS); 14 mi. N of Hyder, foot of Salmon R. Glacier, *T. T. McCabe 8521* (UC); Fox Bay, *D. Martel 146* (WS, WTU); Olga Bay, *E. & B. Loof 289* (BH, DAO, GH, ND, NY, OSC, TRT); Popof Island, *T. Kincaid in 1899* (US); Uyak, *W. Jepson 399* (UC, US); Hot Springs, *T. Howell 1626* (MIN, MO, NY, ORE, UC, US); Prince William Sound, beach of Passage Canal at Whittier, *A. M. Harvill 730* (UNA); Unga Island, *R. Grigas in 1918* (US); Revillagigido Island, Brushy Peak, *M. W. Gorman in 1890* (NDG); Yes Bay, *M. W. Gorman 24* (ORE, WTU); entrance of Disenchantment Bay, *F. Funston 76* (CAN, CU, GH, H, KANU, MO, NY, ORE, US); Chignik, *C. Flock in 1934* (DS); Cleveland Peninsula, Helm Bay, *J. Flett 1987* (US); Washington Bay, Kuiu Island, *W. Eyerdam 7358* (OSC), *7583* (ID); Knight Island, Thum Bay, *W. Eyerdam 3591* (NA); Wrangel, *W. Evans 97* (US); Katlian Bay, Tongass, *Mrs. J. C. Dort 41* (UC); Copper R. Delta, Eyak R. Trail, *J. H. Crow in 1965* (WS); Kukak Bay, *F. Coville & T. Kearney, Jr. 1620* (US); Sand Point, *L. Cole in 1941* (WIS); St. Paul Island, *L. Cole in 1941* (WIS); vicinity of Loring, *F. Chamberlain 102* (US); Trail to Santa Ana, *F. Chamberlain 39* (US); Kenai Peninsula, Mt. Marathon, Seward, *J. A. Calder 6368* (DAO, GH, UC); Ptarmigan Lake near Kenai Lake, *J. A. Calder 6037* (DAO, NY); Gustavus, Glacier Bay National Monument, Excursion Inlet, *D. B. Butts in 1962* (DS); Shumagin Islands, *D. Martel 147* (NY); Sitka, *J. Anderson 100* (US). ARIZONA: APACHE COUNTY, W of Greens Peak at C. C. Cabin, *Pinkava et al. L19170* (ASU), 8 mi. E of Nutrioso, Escudilla Mts., Milk Canyon, *K. F. Parker & E. McClintock 7511* (ARIZ, CAS, COLO, IA, ILL, MO, NY, OKLA, RSA, UC, US, WS), NE¼, Sec. 19, T7N, R27E, along Becker Creek, *C. E. Granfelt 70-180* (ARIZ), Apache Forest, Greer, *W. W. Eggleston 17151* (FSU, GH, NY, US). COLORADO: BOULDER COUNTY, 14 mi. NW of Boulder, *C. Bird 10871* (UAC), Peaceful Valley, Middle Street at C. C. Camp, *L. Bougere 1854* (SMU), S Boulder Canyon, *F. Ramaley 3854* (COLO); CLEAR CREEK COUNTY, Idaho Springs, 2.5 mi. E, *Johnston & Hedgcock 951* (RM); GILPIN COUNTY, Mts. near Golden, *E. L. Green in 1871* (NDG); LAKE COUNTY, near Leadville, *L. M. & N. T. Schedin s.n.* (RM); LARIMER COUNTY, 1 mi. S of Rustic, *P. Ginter 265* (NA), Moraine Park, *G. E. Osterhout 36518* (WIS), Estes Park, Thompson Canyon, *G. E. Osterhout 678* (NY, RM), Rocky Mountain National Park, Big Thompson Creek, *M. F. Colson 72-32* (COLO); PARK COUNTY, Estabrook, *J. P. Young in 1919* (CM, CU); TELLER COUNTY, Green Mt. Falls, *E. Bessey in 1895* (NY); COUNTY UNKNOWN, vicinity of Pine Grove, *C. S. Crandall 1360* (MONTU, NEB, US, WS), Dome Rock in Platte Canyon, *M. E. Jones in 1878* (IA, NA, NY, POM,

UTS). CONNECTICUT: FAIRFIELD COUNTY, Huntington, *E. H. Eames 5110* (NEBC); HARTFORD COUNTY, Southington, Savage Street, *C. Bissell in 1901* (GH, NY); LITCHFIELD COUNTY, 0.28 mi. W of rte 63 on Conn. rte 4, *D. E. Boufford & H. E. Ahles 18841* (KYO, MO), 1.2 mi. E of U.S. rte 7 on Conn. rte 4, *D. E. Boufford & H. E. Ahles 18838* (MHA, MO); MIDDLESEX COUNTY, Portland, *B. Chamberlain in 1924* (NY); NEW HAVEN COUNTY, New Haven, Mt. Carmel, *W. Safford 180* (US); NEW LONDON COUNTY, Ledyard, near Lantern Hill, *W. A. Setchell in 1887* (UC); TOLLAND COUNTY, Somers, *A. S. Pease 920* (NEBC); WINDHAM COUNTY, S Woodstock, *H. Dunslow in 1937* (NY). DISTRICT OF COLUMBIA: Washington, *F. Blanchard in 1892* (NY). IDAHO: BOUNDARY COUNTY, Mission Creek near Copeland, *J. H. Ehlers & C. O. Erlanson 375* (MICH), Brush Creek near Copeland, *J. H. Ehlers & C. O. Erlanson 284* (MICH); IDAHO COUNTY: Bitterroot National Forest, Macgruder Crossing on the Selway R., *J. H. Christ 12747* (NY). ILLINOIS: JO DAVIESS COUNTY, Warren, *L. M. Umbach in 1896* (MIN, PH); KANE COUNTY, Elgin, *G. Vasey s.n.* (ILL); LAKE COUNTY, Lake Bluff, *E. J. Hill 42,1908* (ILL). INDIANA: ALLEN COUNTY, ca. 8 mi. SW of Fort Wayne, *C. C. Deam 50211½* (IND, WIS); LAGRANGE COUNTY, ca. 3 mi. SE of Mongo, *C. C. Deam 50702* (IND); LAPORTE COUNTY, 0.5 mi. E of Andry stop on S Shore Traction Line, *C. C. Deam 31453* (IND); MONTGOMERY COUNTY, along Sugar Creek near the "Shales," *C. C. Deam 9332* (IND); PORTER COUNTY, Tamarack stop on the S Shore Electric Line, *C. C. Deam 8816* (IND); STEUBEN COUNTY, 0.5 mi. E of Bass Lake, *C. C. Deam 1281* (IND, MIN, UC, US). IOWA: ALLAMAKEE COUNTY, Village Creek, Center Township, *T. G. Hartley 7632* (RSA); CLAYTON COUNTY, around Ice Cave, Bixby State Park, *J. H. Schaffner in 1933* (OS); DUBUQUE COUNTY, Liberty Township, 2 mi. W, 2 mi. N of Luxemburg, *L. Smith 9903* (ISC, TEX); MUSCATINE COUNTY, Wild Cat Den, *L. H. Pammel & F. Reppert 1873* (MIN); WINNESHIEK COUNTY, Bluffton, *W. L. Tolstead in 1933* (COLO, NEB, PAC, UC). KENTUCKY: EDMONSON COUNTY, Pine Hollow, ca. 1 mi. from Poplar Springs Church, *K. A. Nicely 1979* (NCSC, NCU); LETCHER COUNTY, Bad Branch, Pine Mt., *E. L. Braun 566* (NY, US), Partridge, Cumberland Valley, *E. L. Braun 1093* (GH, US). MAINE: ANDROSCOGGAN COUNTY, E Auburn, *E. D. Merrill 363* (NEBC); AROOSTOOK COUNTY, ca. 0.25 mi. from Ludlow town line in Houlton, *R. M. Downs 2350* (NCSC), Fort Fairfield, *M. L. Fernald in 1893* (NEBC), St. Francis, *M. L. Fernald in 1893* (NEBC), Monticello, *M. L. Fernald & B. Long 14211* (MO, NEBC, PH), Fort Kent, *K. K. Mackenzie 3357* (NY, US), Aroostook R., T9, R7, *E. Ogden & G. Chamberlain 2649* (US), St Johns R., 3 mi. SE of Van Buren, *G. B. Rossbach 5510* (NCU, WVW), Presque Isle, *F. C. Seymour 23278* (NEBC); CUMBERLAND COUNTY, Westbrook, *P. Ricker 269* (US); FRANKLIN COUNTY, Greenvale, Rangely Lake region, *K. Furbish in 1894* (NEBC), Phillips, valley of Sandy R., *K. Furbish in 1894* (NEBC), Madrid, *C. H. Knowlton in 1917* (PH), Day Mt., Arm Township, *C. D. Richards 5361* (ACAD); Hancock County, Morrison's Campground, E Swan Island, *G. B. Rossbach 6872* (WVW); KENNEBEC COUNTY, E Winthrop, *N. C. Fassett 15841* (KYO); KNOX COUNTY, SE part of Sheep Island, Muscle Ridge, *G. B. Rossbach 3820* (NCU); LINCOLN COUNTY, Ocean Point, *N. C. Fassett 3561* (DUKE, WIS, WS); OXFORD COUNTY, Bowmantown Township, *J. Carter 643* (NHA); Mason, Pickett Henry or Pine Mt., *A. R. Hodgdon & F. S. Steele 10743* (NEBC), Hartford, *J. Parlin in 1885* (NEBC), NW Bethal, Besse Mt., *L. Wheeler 572203* (NEBC), 5 mi. NW of Andover, *R. True 1544* (PENN); PENOBSCOT COUNTY, Clifton, *F. P. Briggs 1483* (RM), Orono, *M. L. Fernald in 1888* (NEBC), Patten, *M. L. Fernald in 1897* (NEBC), near McLeod's, *M. L. Fernald in 1900* (GH, NEBC, PH), Charleston, *O. Knight in 1905* (NMC, NY), Mt. Harris, S Dixmont, *G. B. Rossbach 2099* (ACAD), junction of Hwy 95 and the Penobscot R., *C. L. Rodgers 73671* (FUGR); PISCATAQUIS COUNTY, Dover, *G. Fernald in 1896* (NEBC), Abbot, *M. L. Fernald & B. Long 14212* (NEBC, PH, US), Mt. Katahdin, Chimney Pd, *H. N. Moldenke 19069* (CAN, MT, NCSC, NY, OSC, WTU), SE end of Chamberlain Lake, *G. B. Rossbach 6485* (ACAD), Greenville, Upper Wilson Pd, *E. Walker 159* (MIN, PENN); SOMERSET COUNTY, Cambridge, *F. Bunker in 1873–8* (NEBC), S of Pleasant Pd, *J. Collins & E. Chamberlain* (NEBC), Norrdgewok, Wilder Farm, *D. S. Conant 3359* (CM, KYO, MHA, MO), Seabrook, St. Johns Pd, *D. Hamm 1853* (NEBC), 10 mi. W of Newport on Hwy 2, *C. L. Rodgers 73634* (FUGR), Baker Lake, T7, R17, *H. St. John & G. Nichols 2398* (CAN, NEBC, NY, US); WALDO COUNTY, Dark Harbor, Islesboro, *F. T. Hubbard in 1897* (FSU, LL, NCU, SMU); WASHINGTON COUNTY, E Machias, *M. Barber in 1898* (NEBC), Cherryfield, *S. F. Blake 4015* (LL), Calais, *M. L. Fernald 2010* (GH, MT, NEBC), Cutler, *K. Furbish in 1902* (NEBC); YORK COUNTY, Kennebunk, *F. C. Seymour 5633* (DUKE, NDA, WIS). MARYLAND: CAROLINE COUNTY, Oakland, *H. N. Twing in 1886* (MIN); GARRET COUNTY, Swallow Falls, *F. Shreve 557* (US). MASSACHUSETTS: BARNSTABLE COUNTY, Sandwich, Spring Hill, *M. L. Fernald & B. Long 18848* (CU, NEBC, NYS, PH); BERKSHIRE COUNTY, 6.1 mi. S of the junction of Mass. Rtes 8 & 123 on 8, *D. E. Boufford & H. E. Ahles 18843* (MO), Cheshire Game Management Area off Wells Road, *H. E. Ahles 75945* (DS); BRISTOL COUNTY, New Bedford, *E. Hervey s.n.* (NEBC); ESSEX COUNTY, Boxford, *F. Hunnewell 8878* (NEBC); FRANKLIN COUNTY, Deerfield, *R. G. Poland in 1954* (MISS); HAMPDEN COUNTY, Granville, Bad Luck Mt., *F. C. Seymour 360* (DUKE, GH, MO, NY); HAMPSHIRE COUNTY, Middlefield, *M. L. Fernald & B. Long 10067* (NEBC, PH); MIDDLESEX COUNTY, Sherborn, "The Narrows," *F. Hunnewell 6782* (NEBC); NORFOLK COUNTY, Needham, Washburn's Pines, *T. Fuller in 1892* (NEBC); WORCESTER COUNTY, Stur-

bridge, *D. Comins in 1930* (NEBC), Petersham, *D. S. Correll & T. Steiger 11201* (DUKE). MICHIGAN: ALGER COUNTY, Miner's Falls, *J. C. Myers 199* (WVA); ALLEGAN COUNTY, Macatawa, *C. Mell 169* (US); ANTRIM COUNTY, Torch Lake, *H. E. Sargent 5828*? (MICH); ARENAC COUNTY, ca. 4.5 mi. NW of Omer, *E. G. Voss 4649* (MICH); BARAGA COUNTY, Big Limestone Mt., L'Anse, *N. C. Fassett 21039* (WIS); BENZIE COUNTY, Benzonia Township, *V. Weadock 94* (MICH); BERRIEN COUNTY, Warren Woods, *B. C. Billington in 1919* (MICH); CASS COUNTY, Silver Creek District, *H. S. Pepoon 1442* (MICH); CHEBOYGAN COUNTY, vicinity of Douglas Lake, *H. A. Gleason & H. A. Gleason, Jr. 34* (GH, ISC, NY, SMU, WVA); CHIPPEWA COUNTY, Chase S. Osborn Preserve of Univ. of Michigan, *R. McVaugh 8776* (DS, MICH, NCSC); CLINTON COUNTY, Hubbardston, *C. F. Wheeler in 1878* (KSC); CRAWFORD COUNTY, vicinity of Grayling, *C. Piper in 1922* (US); DELTA COUNTY, 4 mi. NE of Nahma, *R. McVaugh 10936* (MICH); DICKINSON COUNTY, ca. 5.5 mi. NNE of Ralph, *E. G. Voss 9945* (MICH); EMMET COUNTY, N of Idlewild, *J. A. Nieuwland in 1932* (ND); GENESEE COUNTY, Flint, *D. Clarke in 187*? (US); GOGEBIC COUNTY, Black River, *C. D. Richards 3427* (ACAD); GRAND TRAVERSE COUNTY, ca. 10 mi. SE of Traverse City, *J. V. A. Dieterle 1352* (MICH); GRATIOT COUNTY, about Alma, *C. A. Davis in 1892* (WS); HOUGHTON COUNTY, N of Chassell, *C. D. Richards 1965* (DAO); IONIA COUNTY, Hubbardston, *E. Smith 25* (US); IOSCO COUNTY, NW of Oscoda, *G. A. Loughridge 4201* (DAO); IRON COUNTY, ca. 1 mi. SE of Elmwood, *E. G. Voss 7695* (MICH); JACKSON COUNTY, *S. H. & D. R. Camp in 1896* (MIN); KENT COUNTY, Cedar Springs, *C. W. Fallan in 1896* (MIN); KEWEENAW COUNTY, Isle Royale, Duncan Bay, *W. S. Cooper 236* (GH, MIN); LEELANAU COUNTY, ca. 1 mi. NW of Tamarack Lake, *E. G. Voss 5119* (MICH); LUCE COUNTY, shore of Lake Superior just W of Deer Par, *R. L. Stuckey 1142* (OS); MACKINAC COUNTY, ca. 0.5 mi. NE of Brevoort, *R. McVaugh 9380* (MICH, MT); MACOMB COUNTY, Washington, *O. Farwell 6204a* (GH); MANISTEE COUNTY, Manistee, *F. P. Daniels in 1900* (UMO); MARQUETTE COUNTY, Turin, *B. Barlow in 1901* (GH, US); MENOMINEE COUNTY, edge of Creek in County Park, *G. Gressl 2654* (NY); MUSKEGAN COUNTY, Lake Harbor, *W. S. Moffat in 1896* (ILL); NEWAYGO COUNTY, Hidden Lake, *C. M. Bozur 3481* (MICH); OAKLAND COUNTY, Rochester, *O. Farwell 3814½* (GH); OCEANA COUNTY, Benona Township, *J. G. Lacy & S. G. Gumina 77018* (MICH); OSCODA COUNTY, ca. 4 mi. NE of Mio, *C. B. Nimke 798* (MICH); OTTAWA COUNTY, Pigeon Lake, *J. A. Nieuwland in 1918* (MT, ND); ROSCOMMON COUNTY; Prudentville, *R. Driesbach 5197* (PH); SAGINAW COUNTY, 5 mi. N of county line, Flint–Saginaw Road, *R. Driesbach 5087* (PH); ST. CLAIR COUNTY, near Port Huron, *C. K. Dodge in 1896* (ND, TENN, UC); SCHOOLCRAFT COUNTY, near Floodwood, *C. K. Dodge in 1915* (MICH); WASHTENAW COUNTY, Ann Arbor, *S. M. Manning in 1885* (MIN); WAYNE COUNTY, Detroit, *L. Foote in 1870* (MICH). MINNESOTA: AITKIN COUNTY, 2 mi. E of Tamarack, *J. W. Moore & F. K. Butters 13507* (MIN); ANOKA COUNTY, 8 mi. E of Bethel in Cedar Creek area, *V. L. Malone 44* (MIN); BECKER COUNTY, Detroit Lakes, *O. A. Stevens in 1933* (CM, DS); BELTRAMI COUNTY, Black Duck, *Mrs. R. Westley in 1918* (ISC), Cass Lake, Squaw Point, *E. L. Nielsen 79* (MIN); BLUE EARTH COUNTY, Madison Lake, *E. P. Sheldon in 1891* (MIN, NY); CARLTON COUNTY, Thompson, *J. H. Sandberg 417* (ARIZ, KSC, MIN, NEB); CASS COUNTY, Lake Kilpatrick, *C. A. Ballard in 1893* (MIN, RM, WIS), 14 mi. W. 3 mi. N of Remer, *S. Stephens & R. Brooks 41977* (KANU, MASS), Gull Lake, *A. P. Anderson A630* (MIN); CHISAGO COUNTY, Center City, *B. C. Taylor T1377* (MIN, RM, US, WS); CLEARWATER COUNTY, Itasca State Park, near Nicolet Lake, *C. R. Janssen 138* (KYO); COOK COUNTY, E end of Mountain Lake, *F. K. Butters 88* (NY), along portage from Alder to E Bearskin Lake, *F. K. Butters & M. F. Buell 476* (GH, MIN, NY, US), Sawbill Lake, T62N, R4W, *J. DeQ & M. W. Briggs 68* (MIN), ca. 1 mi. N of Mineral Center, *F. R. & J. S. Benner 657* (MIN), Kimball Lake Campground, *E. Loula 14* (MIN), Grand Portage, *P. A. Rydberg 9683* (NY); CROW WING COUNTY, Garrison Township, W side of Chandler Lake, *J. W. & M. F. Moore 256* (MIN); DOUGLAS COUNTY, 1 mi. NE of Spruce Center, *C. R. Sperling 359* (NDA); HENNEPIN COUNTY, Deephaven, Minnitonka, *C. O. Rosendahl 1271* (MIN); HOUSTON COUNTY, Sec. 16, Mayville Township, *F. K. Butters & C. O. Rosendahl 3935* (MIN); HUBBARD COUNTY, *R. Bebb 4754* (MO, OKL, OKLA, SMU); ISANTI COUNTY, W of the Lindgren Farmstead, *J. W. Moore & F. B. Abeles 25192* (MIN); ITASCA COUNTY, hwy 6, 4 mi. S of the junction with the road from Big Fork, *J. W. Moore & R. B. Hall 16772* (DAO, MIN), between Cut Foot Sioux and Inger, *A. Johnson 3228* (PH), ca. 8.5 mi. SW of Grand Rapids, *G. A. Wheeler & P. H. Glaser 2008* (DUR), Bowstring, *H. E. Stork 1214* (MIN); KOOCHICHING COUNTY, Rainy Lake, E side of Tilson Bay, *J. W. & M. F. Moore 11840* (MIN); LAKE COUNTY, Sec. 20, T64N, R10W, *C. Ahlgren 159* (MIN, TRT), ca. 14 mi. W of Finland, near S end of Cloquet Lake, *E. G. Voss 10065* (MICH, MIN, VDB), inlet to Moose Lake Canadian Border Lodge, *O. Lakela 16513* (DUL, MIN), Superior National Forest, Quetico-Superior Wilderness, *W. L. Baxter in 1956* (DAO), Upper Manitou Falls, *G. & F. Ownbey 977* (H, NY), 5 mi. E of Two Harbors, *H. A. Gleason 9557* (NY); LAKE OF THE WOODS COUNTY, Lake of the Woods, 3 mi. S of Rocky Point, *C. O. Rosendahl et al. 7016* (MIN), Angel Inlet, *J. W. & M. F. Moore 11101* (MIN); MAHNOMEN COUNTY, Oakland Township, *M. Partch in 1958* (MIN); MILLE LACS COUNTY, Milaca, *E. P. Sheldon in 1892* (MIN, RM, WIS); OTTERTAIL COUNTY, 3 mi. N of Battle Lake, *P. Johnson 538* (GH, IA, NY, UMO), Dora Township, between Dillers Pd and Star Lake, *P. Jones 374* (GH);

Pine County, near the NE corner of St. Croix State Park, *J. W. Moore & N. L. Huff 18083* (MIN); ROSEAU COUNTY, Roseau, *W. E. Manning in 1923* (CM); ST. LOUIS COUNTY, Duluth, *O. Lakela 2579* (MIN, MO, OKLA, SMU, UC), Anttila Farm, Palo, *O. Lakela 2621* (DUL, MIN, WS), Kabetogama Lake, Pine Island, *O. Lakela 14958* (DUL, MIN); STEARNS COUNTY, Collegeville, *P. E. Kuehne in 1933* (DAO); WRIGHT COUNTY, "Big Woods" W of Delano, *F. K. Butters & C. O. Rosendahl 3349* (MIN). MONTANA: FLATHEAD COUNTY, Glacier National Park, Avalanche Campground, *L. H. Harvey 5183* (MONTU), Mt. Cannon above McDonald Creek, *L. H. Harvey 6064* (NCU), W side of Glacier National Park, *W. McCalla 3784* (ALTA), 1 mi. S of Columbia Falls, *H. T. & J. M. Rogers 1234* (MO, NY, WS, WTU), Big Fork, *Mrs. J. S. Clemens in 1908* (CAS); GALLATIN COUNTY, Bozeman & vicinity, Spring Hill, *J. Blankinship in 1905* (MONTU), Bozeman, Leverich Canyon, *W. E. Booth in 1956* (DAO, RM, WTU); GRANITE COUNTY, Rock Creek Canyon, *C. L. Hitchcock & C. V. Muhlick 14394* (WTU); LAKE COUNTY, T23N, R18W, Sec. 24, *J. R. Habeck in 1962* (WTU), Flathead Lake, Swan Lake, *M. E. Jones 8402* (MONTU), Flathead Lake, *A. W. L. Bray in 1914* (OS); LEWIS & CLARK COUNTY, Blue Cloud near Helena, *F. Kelsy 546* (NY); MISSOULA COUNTY, ca. 12 mi. from mouth of Miller Creek Canyon, *C. L. Hitchcock 1772* (MONTU, POM), Lolo, near Woodman, *J. Kirkwood 1216* (MICH, MONTU, ORE, UC), 5 mi. NW of St. Regis Junction, *K. M. Wiegand et al. 1747* (CU), Missoula, Marshall Gulch, *? in June 1915* (DS, ISC); RAVALLI COUNTY, Bitterroot Mts. off lower St. Mary's Road, *K. H. Lakschewitz 5124* (COLO); ROSEBUD COUNTY, First Lake, E Rosebud R., *P. Hawkins in 1921* (WIS). NEW HAMPSHIRE: BELKNAP COUNTY, Gilmanton, *J. Cushman & S. Sanford 1220* (LL, NEBC); CARROLL COUNTY, Madison, *A. R. Hodgdon et al. 9598* (UNA); CHESHIRE COUNTY, town of Chesterfield, "The Gulf," *D. E. Boufford 18855* (C, G, KYO, MHA, MO, PE); COOS COUNTY, Lancaster, *A. S. Pease 14328* (NEBC), Pittsburg, Norton Pool at E Inlet, *A. R. Hodgdon & P. Allen 18302* (NHA); GRAFTON COUNTY, Hanover, *H. Barss in 1910* (OSC); HILLSBOROUGH COUNTY, Newburg, Mt. Sunapee, *F. B. Rousseau 1722* (MO); ROCKINGHAM COUNTY, Raymond, *A. R. Hodgdon & R. Leighton 5767* (NEBC); STRAFFORD COUNTY, Rollinsford, *A. R. Hodgdon 11910* (NEBC); SULLIVAN COUNTY, 6.9 mi. E of Grantham, *H. E. Ahles 68466* (MASS). NEW JERSEY: MORRIS COUNTY, 3 mi. S of Melton, *C. Williamson in 1905* (PH); SUSSEX COUNTY, Sparta Glen, *K. K. Mackenzie 4221* (MO, NY, US); WARREN COUNTY, 0.5 mi. NE of Uniontown, *R. Shaeffer, Jr. 44375* (US). NEW MEXICO: Catron County, Mogollon Mts., on or near the W Fork of the Gila R., *O. B. Metcalfe 516* (ARIZ, GH, ILL, MASS, MIN, MO, NDG, NMC, NY, RM, US). NEW YORK: ALBANY COUNTY, E. N. Huyck Preserve, Rensselaerville, *N. H. Russell 6255419* (IA, TENN); CATTARAUGUS COUNTY, Conewango, *E. Anderson & R. Woodson, Jr. 816* (MO); CAYUGA COUNTY, Conquest, NE end of Duck Lake, *L. H. MacDaniels 6934* (CU); CHATAUQUA COUNTY, Forestville, *E. A. Southworth in 1885* (MICH); CHEMUNG COUNTY, Laurel Hill, *S. J. Smith 460* (CU); CHENANGO COUNTY, Norwich, *M. H. Fitch in 1890* (POM); COLUMBIA COUNTY, Cofake Mt. Alander, *R. McVaugh 1775* (PENN); DELAWARE COUNTY, vicinity of N Harpersfield, *D. Topping 184* (US); DUTCHESS COUNTY, North East, N of Mt. Brace summit, *H. D. House 24827* (NY); ERIE COUNTY, E of Gowanda, *W. C. Muenscher 15801* (CU); ESSEX COUNTY, near Newcomb, *H. D. House 9117* (CAS); FULTON COUNTY, Casoga, *H. Dunslow in 1932* (NY); FRANKLIN COUNTY, Pinehurst, *K. Guest 257* (PENN); GENESEE COUNTY, Berger Swamp, *W. C. Muenscher & B. I. Brown 21370* (CU); GREENE COUNTY, near Hunter, *N. L. Britton in 1898* (NY); HAMILTON COUNTY, 0.9 mi. SW of Bear Brook, *G. H. M. Lawrence & W. J. Dress 385* (BH, DAO); HERKIMER COUNTY, Little Moose Lake, *S. van Pelt in 1906* (PH); JEFFERSON COUNTY, Pierrepont, *O. Phelps 716* (GH, US); LEWIS COUNTY, NW of Rector, *N. Hotchkiss 206* (NYS); MADISON COUNTY, Valley Mills, *H. D. House 1153* (MO, US); MONROE COUNTY, Ontario lowlands N of Webster, *W. A. Matthews 4166* (NCU, UC); NIAGRA COUNTY, Wilson, *A. D. Pease 893* (DAO); ONEIDA COUNTY, White Lake *R. McVaugh 32* (PENN); ONONDAGA COUNTY, Syracuse, *M. L. Overacker in 1889* (KSC); ONTARIO COUNTY, Canadaigua, *E. J. Durand in 1892* (MIN); ORANGE COUNTY, Greenwood Lake, *J. Schrenk in 1876* (CU); ORLEANS COUNTY, Oak Orchard, *S. Flirtham in 1897* (BH); OSWEGO COUNTY, Volney, *L. M. Howard in 1916* (CU); OTSEGO COUNTY, along Summit Lake, *W. C. Muenscher & O. F. Curtis, Jr. 5259* (CU); RENSSELAER COUNTY, S of Petersburg Pass, *H. D. House 21634* (CU, NY, PENN); ST. LAWRENCE COUNTY, Hopkinton, Fort Jackson, *L. Harper in 1932* (CU); SARATOGA COUNTY, S of Wilton, *H. D. House 29873* (TEX); SCHOHARIE COUNTY, Sharon Springs, *M. Brandegee s.n.* (UC); SCHUYLER COUNTY, Walkins Glen, *A. J. Eames 2928* (CU); SENECA COUNTY, Duck Lake, near N end of Cayuga Lake, *P. A. Munz 756* (POM); SULLIVAN COUNTY, Ten Mile R., *W. A. Weber 1054* (COLO); STEUBEN COUNTY, W side of Waneta Lake, *R. T. Clausen 1369* (BH, UC); TIOGA COUNTY, Richford, NE of Caroline, *A. Gershoy 10509* (CU); TOMPKINS COUNTY, Slaterville, along Six Mile Creek, *G. H. M. Lawrence 463* (KY, WTU); ULSTER COUNTY, Hwy 28 between Big Indian & Shandaken, *E. Haber 661* (TRT); WARREN COUNTY, 3 mi. N of Luzerne, *M. Tees in 1936* (PH); WASHINGTON COUNTY, between hills of Pilot Knob-Sugar Loaf Mt. range, *W. T. Winne in 1941* (B, GA, ISC, OSC, UARK); WAYNE COUNTY, E of Clyde, *F. P. Metcalf 8525* (CU, GH); WESTCHESTER COUNTY, 2–3 mi. below Bedford, *W. Pennell 7122* (PH); WYOMING COUNTY, Gainesville, *D. S. Jordan in 1870* (CU); YATES COUNTY, Five Mile Swamp, Five Mile Creek, *W. C. Muenscher 23592* (CU). NORTH CAROLINA: ASHE

COUNTY, near N Fork New R., Bins, *A. E. Radford 38574* (NCU); AVERY COUNTY, in balsam grove on Roan Mt., *M. L. Smyth 3152* (VPI); BUNCOMBE COUNTY, Craggy Mountain, *Biltmore Herb. 1967b* (GH, ISC, MICH, MIN, MO, NCSC, NCU, NY, NYS, OS, TUR, US, VT, W); CLAY COUNTY, Perry Gap Road 2.7 mi. N of U.S. 64, *J. Massey et. al. 4712* (NCU, WCUH); GRAHAM COUNTY, Joyce Kilmer Memorial Forest, *W. C. Coker & L. M. Stewart in 1939* (NCU); HAYWOOD COUNTY, Mt. Sterling, *D. C. Bain & H. M. Jennison 1097* (TENN); JACKSON COUNTY, Rough Butt Bald Mt., *G. S. Ramseur 241* (CM); MACON COUNTY, Highlands, Dry Falls, *E. Quarterman 981* (VDB); MADISON COUNTY, 3.5 mi. SE of Trust on N.C. 36, *H. E. Ahles & J. A. Duke 46483* (DAO, NCU, VDB); MCDOWELL COUNTY, near Big Craggy on the Blue Ridge Parkway, *C. R. Bell 4440* (FSU, GA, NCU); MITCHELL COUNTY, Roan Mt., fir forest, *A. E. Radford 45000* (AUA, CM, DAO, DHL, FSU, FUGR, GA, GAS, GH, H, IND, ISC, KE, KY, LL, LYN, MISS, NCU, NDA, NY, OSC, PAC, RSA, SMU, STAR, TENN, TEX, TRT, UARK, UBC, UC, UNA, UNCC, US, VDB, VSC, WCUH, WILLI, WIS, WVA); SWAIN COUNTY, near Leatherman's Gap, *A. E. Radford 6420* (PAC, SMU, US); TRANSYLVANIA COUNTY, NE slope of Fryingpan Mt., *O. M. Freeman 57590* (NCU, VPI); WATAUGA COUNTY, Sim's Trail near Blowing Rock, *M. L. Smyth 2546* (VPI); YANCEY COUNTY, Balsam Gap, W of the Blue Ridge Parkway, *W. B. Fox 5011* (BHO, NCSC, PH, SMU). NORTH DAKOTA: BARNES COUNTY, Kathryn, *H. F. Bergman 2285* (CAN, MIN, NDA); BENSON COUNTY, Plesant Lake, *J. Lunell in 1912* (MIN, NY, SDU, US); PEMBINA COUNTY, Walhalla, *O. A. Stevens 257* (DAO, GA, MT, NDA, NY, OKL, SMU, UC, WIS); ROLETTE COUNTY, Turtle Mts., *O. A. Stevens in 1942* (NDA). OHIO: ALLEN-VAN WERT COUNTIES, Delphos, *H. Young in 1884* (GH); ASHLAND COUNTY, Mohican State Forest, Hanover Township, *T. S. Cooperrider 8283* (KE); ASHTABULA COUNTY, 2 mi. WSW of Windsor, *T. S. Cooperrider 8567* (KE); CLARKE COUNTY, Springfield, *Mrs. E. J. Spence in 1879* (OS); COLUMBIANA COUNTY, Yellow Creek Township, *T. S. Cooperrider & B. Hoffman 6381* (KE); COSHOCTON COUNTY, White Eyes Township, *A. W. Cusick 5819* (KE, NCU); CUYAHOGA COUNTY, Cleveland, *W. Krebs & E. Claassen in 1890* (OS); ERIE COUNTY, Florence Township, *E. L. Moseley in 1898* (US); FRANKLIN COUNTY, Worthington, *A. Horr s.n.* (ISC); GEAUGA COUNTY, Bainbridge Township, *T. S. Cooperrider & E. Hauser 8531* (KE); HOCKING COUNTY, Gibsonville, *J. D. & W. A. Wistendahl 742* (BHO); HOLMES COUNTY, Washington Township, *T. S. Cooperrider 8131* (KE); HURON COUNTY, Olena, *O. E. & G. K. Jennings in 1906* (CM); JACKSON COUNTY, Liberty Township, *F. Bartley in 1969* (BHO); JEFFERSON COUNTY, Island Creek Township, *A. W. Cusick 8193* (KE); KNOX COUNTY, Jefferson Township, *P. L. Pusey 623* (KE, OS); LAKE COUNTY, near Painesville, *W. C. Werner 6068* (OS); LORAIN COUNTY, Oberlin, *A. E. Ricksecker in 1894* (OS, US); MEDINA COUNTY, 1.5 mi. E of Sharon Center, *T. S. Cooperrider & E. Herrick 7487* (KE); MORGAN COUNTY, Fairfield Township, *G. M. Silberhorn 4548* (KE); PORTAGE COUNTY, Freedom Township, *A. N. Rood & R. J. Webb 145* (KE); SUMMIT COUNTY, Twinsburg, Crown Hill Memorial Park, *E. M. Herrick in 1955* (OS); TRUMBULL COUNTY, Mesopotamia Township, Casey's Spring, *D. E. Boufford 18820* (KYO, MHA, MO). PENNSYLVANIA: ALLEGHENY COUNTY, 1 mi. W of Glenshaw, *O. E. Jennings 6250* (CM); BEDFORD COUNTY, 0.5 mi. WSW of Wolfsburg, *D. Berkheimer 20262* (CM); BERKS COUNTY, 2.12 mi. W of Wernersville, *D. Berkheimer 2120* (CM); BLAIR COUNTY, 5.2 mi. N of Tipton, *W. E. Buker in 1972* (CM); BRADFORD COUNTY, 13 mi. E of Canton, *W. F. Westerfeld 938* (CM, PAC, PH); BUTLER COUNTY, 2 mi. N of Slippery Rock, *O. E. Jennings in 1922* (CM); CAMBRIA COUNTY, 1.3 mi. W of Nicktown, *L. K. Henry & W. E. Buker in 1954* (CM); CAMERON COUNTY, 5 mi. NW of Emporium, *J. M. Fogg et al. 20212* (CM); CARBON COUNTY, in Glen Onoko, *H. W. Pretz 1965* (NY, PH, VPI); CENTRE COUNTY, Bear Meadows, *L. K. Henry & W. E. Buker in 1950* (CM); CLARION COUNTY, valley of river at Clarion, *O. E. Jennings in 1921* (CM); CLEARFIELD COUNTY, N Gerard Township, *L. K. Henry in 1941* (CM); CLINTON COUNTY, Lamar Township, *D. E. Boufford 18830* (BM, CM, G, GH, K, KYO, LD, MHA, MO, P, PE, S, UC); COLUMBIA COUNTY, North Mts. above Ricket's, *H. Meredith in 1920* (PH); CRAWFORD COUNTY, Conneaut Lake, *J. A. Shafer 275* (CU, ISC, MICH, MT, NCU, NDA, NLU, OKLA, PH, UC, US); DAUPHIN COUNTY, 2.5 mi. SSE of Enterline, *D. Berkheimer 14702* (PAC, PENN); ELK COUNTY, Spring Creek Township, *A. N. Rood & W. Simon 641* (KE); ERIE COUNTY, LeBoeuf Lake, *L. K. Henry & W. E. Buker in 1953* (CM); FAYETTE COUNTY, Ohiopyle, *P. Ricker 1223* (US); FOREST COUNTY, ca. 2 mi. S of Duhring, *L. K. Henry in 1955* (CM); FRANKLIN COUNTY, 3 mi. W of Roxbury, *E. Earle 2715* (PENN); HUNTINGDON COUNTY, Owl's Hollow, *T. C. Porter in 1878* (PH); INDIANA COUNTY, 2 mi. above Chambersville on rte 110, *L. K. Henry in 1941* (CM); JEFFERSON COUNTY, Sigel Township, *D. E. Boufford 18826* (KYO, MO, PE); LACKAWANNA COUNTY, 0.5 mi. W of Dalton, *S. L. Glowenke 8528* (MIN); LANCASTER COUNTY, *J. Galen 893* (CAS); LAWRENCE COUNTY, near Eckert's Bridge, Slippery Rock Creek, *H. W. Graham in 1923* (CM); LEBANON COUNTY, 2.5 mi. SE of Millbach, *H. Wilkens 8292* (PENN); LEHIGH COUNTY, Bethlehem, Lehigh Mt., *J. Wolle in 1841* (CM); LYCOMING COUNTY, 2 mi. WNW of Waterville, *E. T. Wherry in 1946* (PH); MCKEAN COUNTY, Mt. Jewett, *O. E. Jennings in 1922* (CM); MERCER COUNTY, 2 mi. NE of Grove City, *O. E. Jennings in 1940* (CM); MIFFLIN COUNTY, Otter Gap, *L. Overholts & H. Popp in 1922* (PAC); MONROE COUNTY, ca. 1.5 mi. SE of Mt. Pocono, *E. C. Earle 1113* (TENN); NORTHAMPTON COUNTY, Bangor (Greenwold), *C. Bachman in 1908* (PH); PIKE COUNTY, Beaver Dam, "Hunting

Tower," *S. Brown & C. Saunders in 1899* (PH); POTTER COUNTY, rte 144 near Ole Bull State Park, *W. E. Buker in 1965* (CM); SCHUYLKILL COUNTY, 1.5 mi. W of Snyders, *P. Wagner 4677* (PENN); SNYDER COUNTY, 3 mi. NNE of Troxelville, *Wade & Wade 1343* (PENN, WIS); SOMERSET COUNTY, ca. 2 mi. NW of Springs, *L. K. Henry in 1968* (CM); SULLIVAN COUNTY, Ganoga Glen, *H. W. Pretz 3931* (VPI); SUSQUEHANA COUNTY, 2 mi. NW of Elkdale, Elk Mt., *R. H. True 4108* (CM); TIOGA COUNTY, Leonard Harrison State Park, *L. K. Henry in 1937* (CM); VENANGO COUNTY, 1 mi. N of Perry Run along Allegheny R., *A. J. Deer in 1933* (CM); WARREN COUNTY, North Warren, *H. N. Moldenke 15427* (CM, ND, OLKA, OSC, VDB); WAYNE COUNTY, 1.5 mi. NE of Cold Spring, *H. A. Wahl 14512* (NCU); WESTMORELAND COUNTY, 7 mi. N of Ligonier, *C. T. Agostini in 1933* (CM); WYOMING COUNTY, W of Dunkhannock, *J. Bright in 1925* (CM). RHODE ISLAND: PROVIDENCE COUNTY, Chapachet, Douglas Hook Road, *R. Champlin in 1973* (NEBC). SOUTH DAKOTA: CUSTER COUNTY, Custer, *P. A. Rydberg 712* (GH, NMC, NY, US), Sylvan Lake, *J. M. Moore 33* (MIN), ravine at SE base of Buckhorn Mt., *A. C. McIntosh 557* (RM, SDU); LAWRENCE COUNTY, 7.5 mi. S of Spearfish, *S. Stephens 7724* (DS, KANU), on road to Terry Peak, *T. Van Bruggen 5894* (SDU); MEADE COUNTY, Piedmont, *A. Pratt in 1895* (MIN, POM, WIS); PENNINGTON COUNTY, Sylvan Lake, *W. Over 15833* (US). TENNESSEE: BLOUNT COUNTY, Gregory Bald, Great Smoky Mountains National Park, *A. J. Sharp 1959* (TENN); CARTER COUNTY, summit of Roan Mt., *K. Rogers & J. K. Underwood 34663* (TENN); COCKE COUNTY, vicinity of Cosby, *J. R. Raper & H. M. Jennison 3263* (TENN); SEVIER COUNTY, Little Pigeon R. at Chimney Caps Trail, *S. A. Cain & A. J. Sharp 650* (MO). VERMONT: ADDISON COUNTY, Middlebury, *C. Knowlton in 1933* (NEBC); BENNINGTON COUNTY, South Shaftsbury on U.S. rte 7, *H. E. Ahles 67929* (DS, MASS, NEB, WVA); CALEDONIA COUNTY, Lyndonville, *D. S. Conant & A. Kitfield 2917* (BM, G, K, KYO, LD, MHA, MO, NY, P, S, SHIN, UC); CHITTENDEN COUNTY, Williston, *S. F. Blake 2552* (LL, US); ESSEX COUNTY, Canaan, rte 114, *F. C. Seymour 25674* (CAS, MO, SMU); FRANKLIN COUNTY, Franklin, *R. Woodward in 1912* (NEBC); LAMOILLE COUNTY, Stowe, Mt. Mansfield, *J. Murdoch, Jr. 1695* (NEBC); ORANGE COUNTY, Brookfield, *F. C. Seymour 22176* (MO); ORLEANS COUNTY, Morgan, Seymour Lake region, *J. Harper 33* (PH); RUTLAND COUNTY, 2.9 mi. E of junction Vt. rte 140 & U.S. rte 7 on rte 140, *H. E. Ahles 68917* (DS, GA, NDA, PAC, US); WASHINGTON COUNTY, Worcester, *W. Blanchard in 1875* (NEBC); WINDHAM COUNTY, Whitingham, *H. E. Ahles 68575* (NLU, UMO); WINDSOR COUNTY, 3.2 mi. S of junction Vt. rte 100 & U.S. rte 4 on rte 100, *H. E. Ahles 68128* (CM, DS, ISC). VIRGINIA: AMHERST COUNTY, Blue Ridge, Elk Pond Mt., *C. E. Stevens 2088* (LYN); AUGUSTA COUNTY, Little R. NW of Stokesville, *B. J. & A. M. Harvill 22163* (FARM); BATH COUNTY, Warm Springs Mt., near Hot Springs, *C. E. Stevens & L. Carr 7588* (FARM); BOTETOURT COUNTY, Appalachian Trail on W side of Rich Mt., *R. S. Freer 2155* (GH, LYN); FLOYD COUNTY, Buffalo Mt., *C. E. Stevens 13001* (FARM); GILES COUNTY, Cranberry bog near White Pine Lodge, *J. W. Hardin 2490* (NCSC, VDB); GRAYSON COUNTY, Saddle on Brier Ridge, *A. R. Shields in 1954* (VPI); GREENE COUNTY, N slope of Bush Mt., Shenandoah National Park, *T. F. Wieboldt 572* (WILLI); HIGHLAND COUNTY, Allegheny Mt., near Bear Mt., *C. E. Stevens & L. Carr 1333* (FARM); MADISON COUNTY, Shenandoah National Park, the Limberlost, *C. E. Stevens 10986* (FARM); NELSON COUNTY, Montebello, grounds of State Fish Hatchery, *R. S. Freer 1874* (GH, LYN); PAGE COUNTY, near Luray, *E. S. & Mrs. Steele 109* (MIN); ROCKBRIDGE COUNTY, Blue Ridge, Elk Pond Mt., *C. E. Stevens 11372* (FARM); ROCKINGHAM COUNTY, Virgin Forest above Skidmore Fork, *A. M. Harvill 20047* (FARM); SMYTH COUNTY, Mt. Rogers, near summit, *R. Kral 11647* (VPI); TAZEWELL COUNTY, Morris Knob, *C. E. Stevens & R. J. Watson 7381* (FARM); WASHINGTON COUNTY, summit of White Top Mt., *J. K. Small in 1892* (MASS). WASHINGTON: FERRY COUNTY, Sherman Creek, 15 mi. W of Kettle Falls, *L. Boner & V. Weldert 238* (DS, UC, UTC, WS); Colville National Forest, just S of Trout Lake, *S. Saufferer 275* (NY); Gray's Harbor County, Road to Olympic National Park S of Lake Quinault, *Cooke et al. W2324* (ASU), Montesano, *J. M. Grant 832* (WS), Lake Quinault, *W. Bailey 2* (WS); JEFFERSON COUNTY, Olympic Peninsula, Quinault R., *Leach & Leach in 1929* (ORE), ca. 18 mi. NE of Quinault *via* Park Road, *V. J. Wetherell 547* (RM), Quinault Valley, 0.25 mi. above lake, *H. S. Conrad 133* (MIN, NEB, NY, PENN, PH, US, WS, WTU), Olympic Peninsula, upper Hoh R., *W. C. Muenscher & B. I. Brown 23242* (CU), Olympic National Forest near Jackson Guard Station, Hoh R., *J. E. Schwartz 11A* (WTU); KING COUNTY, Seattle, *E. A. Shumway in 1892* (WTU), Kings Lake, 1 mi. W of Boyle Lake, NE of Snoqualmie Falls, *G. Ledbednik 383* (WTU), Snoqualmie Falls, *C. Piper 3804* (GH, NY, US, WS); KITTITAS COUNTY, valley of Swauk R., *S. Sharples 156* (GH); SKAGIT COUNTY, near Prairie P.O., *H. R. Talcott in 1891* (MICH), Bear Creek near Concrete, *L. R. Mason in 1932* (UC); SNOHOMISH COUNTY, Cascade Mts., Big Four Inn, *J. W. Thompson 14701* (ALTA, CAN, CAS, GH, MO, NA, NY, PH, RSA, UC, US, W, WS), Snoqualmie National Forest, *E. A. Purer 7718* (DS, WIS), Index, *T. E. Savage et al. in 1898* (COLO, IA, MO, PH, WS); SPOKANE COUNTY, Rock Creek near Mica Peak, *W. N. Suksdorf in 1889* (WS); WHATCOM COUNTY, Baker to Mt. Baker, *W. Bailey in 1908* (WTU), ca. 3 mi. NW of Baker Lake, *G. W. Douglas 1431* (DAO), Mt. Baker National Forest, Baker Hot Spring, *W. C. Muenscher 8266* (CU, GH, WS), Swift Creek, *W. C. & M. W. Muenscher 5981a* (CU), Fairhaven, *W. N. Suksdorf in 1890* (WS). WEST VIRGINIA: FAYETTE COUNTY, Babcock

State Park, *W. N. Grafton & C. McCraw in 1973* (WVA); GRANT COUNTY, 1 mi. S of Bismark, *C. L. Clarke 291* (WVA); HARDY COUNTY, Trout Run where trail leaves Wardensville Hwy for Sugar Knob Shelter, *H. A. Allard 6808* (WVA); MONONGALIA COUNTY, Cheat, Morgantown, *B. D. Barclay in 1925* (WVA); PENDLETON COUNTY, Spruce Knob, *A. J. Sharp 138* (KSC, MO, NA, NCSC, NY, OSC, PENN, SMU, UC, VPI, WVA); POCAHONTAS COUNTY, Cranberry, *G. Guttenberg in 1877* (CM); PRESTON COUNTY, Terra Alta, *B. Quantz in 1937* (WVA); RALEIGH COUNTY, Glade Creek, ca. 2 mi. above the bridge where rte 3 crosses, *J. P. Tosh 834* (US, WVA); RANDOLPH COUNTY, on top of Cheat Mt., *R. B. & J. Clarkson 599* (MAK); SUMMERS COUNTY, Keeney Knob, *West Virginia Univ. Bot. Exped. in 1928* (WVA, WVW); TUCKER COUNTY, Canaan Valley, on top of Bald Knob, *H. A. Allard 19683* (US); UPSHUR COUNTY, Canaan Valley, *J. S. Netting in 1933* (CM); WEBSTER COUNTY, Camp Caesar, *West Virginia Univ. Bot. Exped. in 1929* (DS, GH). WISCONSIN: ADAMS COUNTY, Big Flats Township, *T. Hartley 5639* (WIS); ASHLAND COUNTY, Apostle Island National Seashore, Basswood Island, *R. G. Koch 8660* (MASS, NLU, UT); BARRON COUNTY, Barron, *C. Goessl 8719* (B, WIS); BAYFIELD COUNTY, ca. 9 mi. N, 2 mi. W of Bayfield, Little Sound Bay, *R. G. Koch 8638* (MASS, UT, WIS); BROWN COUNTY, Scott, *J. Schuette in 1897* (NY); CALUMET COUNTY, *W. A. Kellerman s.n.* (OS); CLARK COUNTY, 5 mi. SE of Worden Township, *M. Bergseng in 1948* (WIS); COLUMBIA COUNTY, near Lost Lake, E end of Baraboo Hills, *N. C. Fassett 22331* (WIS); DANE COUNTY, Madison, *L. Cheney s.n.* (WIS); DOOR COUNTY, Washington Island, *A. Fuller 1433* (WIS); DOUGLAS COUNTY, ca. 1 mi. N of Solon Springs, *R. G. Koch 5797* (MASS, UT); DUNN COUNTY, Menomonie, *C. Goessl 9029* (B); FLORENCE COUNTY, 6 mi. ENE of Long Lake, *H. H. Iltis et al. 20421* (OSC, WIS); FON DU LAC COUNTY, Kettle Morain Forest, Marthe L., *H. H. Iltis & W. Buckman 10770* (WIS); FOREST COUNTY, Argonne Experimental Forest, *G. W. Thomson 46* (ISC); GRANT COUNTY, T6, R1W, Sec. 11, NE¼, *T. S. Cochrane 5567* (WIS); IOWA COUNTY, ca. 2 mi. S of Mineral Point, *S. C. Wadmond in 1935* (MIN); IRON COUNTY, ca. 8 mi. S of Hurley, *R. G. Koch 9695* (NLU); JACKSON COUNTY, 6 mi. NE of B. N. Falls, *D. Grether 6325* (WIS); JUNEAU COUNTY, Lyndon Township, *T. Hartley 4214* (WIS); KEWAUNEE COUNTY, near Algoma, *E. J. Palmer 28819* (MO, UMO); LACROSSE COUNTY, Washington Township, *T. Hartley 734* (IA, WIS); LINCOLN COUNTY, Harrison Township, *Wild Flower Club in 1955* (WIS); MANITOWAC COUNTY, Cooperstown, Maribel Caves, *N. C. Fassett 18522* (UBC, WIS, WS); MARATHON COUNTY, near Granite Heights, *L. Cheney 3030* (WIS); MARINETTE COUNTY, near Peshtigo, *C. O. Grassl in 1936* (MICH); MARQUETTE COUNTY, bluff above Lawrence Creek, *P. D. Sorenson 1605* (IA); MENOMINEE COUNTY, Valley of the Giants, *G. Goff in 1964* (NCU); MILWAUKEE COUNTY, N Greenfield, *R. M. Strong in 1892* (KSC); OCONTO COUNTY, T32N, R15E, Sec. 35, *R. & D. Schlising 1032* (WIS); ONEIDA COUNTY, American Legion State Forest, Clear Lake, *P. B. Whitford 1893* (IA); OUTAGAMIE COUNTY, Grand Chute, *F. C. Seymour 10250* (KANU); OZAUKEE COUNTY, N side of small Lake, S of Newburg, *W. W. Oppel et al. 604* (UC, WIS); PEPIN COUNTY, E of Durand, Chippewa R. valley, *C. O. Rosendahl & F. K. Butters 3113* (MIN); POLK COUNTY, St. Croix Falls, *C. F. Baker in 1900* (DS, POM); PRICE COUNTY, 4.5 mi. E of Ogema along Wisc. 86, *H. H. Iltis & W. Buckman 11686* (GA, WIS); RACINE COUNTY, 1 mi. NE of Ives, *S. C. Wadmond 3228* (MIN); RICHLAND COUNTY, 4 mi. NE of Ithaca, *M. Nee in 1974* (WIS); ROCK COUNTY, Beloit, Rock R. Valley, *G. Swezey s.n.* (WIS); RUSK COUNTY, T34N, R8W, Sec. 19, *R. Anderson in 1962* (WIS); ST. CROIX COUNTY, Apple R. Canyon 2 mi. upstream from St. Croix R. junction, *N. Russell in 1948* (MIN); SAUK COUNTY, Parfrey's Glen, Merrimac, *W. V. Grotjan 103* (TENN); SAWYER COUNTY, Pickerel Lake (Lake of the Pines), *H. H. Iltis 20612* (WIS); SHAWANO COUNTY, 1 mi. N of Loon Lake, *J. Gunderson 230* (WIS); SHEBOYGAN COUNTY, Sheboygan, Andrae State Park, *A. Fuller 220* (WIS); TAYLOR COUNTY, 1.5 mi. NW of Rib Lake, *O. Anderson 195* (OKLA, WIS); VERNON COUNTY, Wildcat Mt. State Park, *T. & R. Hartley 1800* (IA, US, WIS); VILAS COUNTY, W of Plum Lake, *J. Marr 221* (MIN); WASHBURN COUNTY, Audubon Camp of Wisconsin, *H. Irwin in 1966* (WIS); WAUSHARA COUNTY, slope above Marl Lake, *P. Sorenson 2219* (IA, WIS); WINNEBAGO COUNTY, Oshkosh, *W. Kellerman s.n.* (US, WIS); WOOD COUNTY, Pittsville, *C. Colby 4510* (CAS). WYOMING: ALBANY COUNTY, Hermosa (SSE of Laramie), *J. F. Macbride 2608* (MO, RM); TETON COUNTY, Grand Teton National Park, along Bradley Creek, *L. Williams 854* (CAS, MO, NA, NY, RM, UTC).

EUROPE

AUSTRIA. Tirol, Karlsteg, above Mayrhoffen, *J. Ball in 1871* (PH); near Plecknerhaus, *J. Ball in 1875* (CAS); Wien, *I. Dorfler s.n.* (ND); Kärnten, Annenheim, *G. Cufodontis in 1970* (W); Siebenburgen, Fogarascher Mts., Bulea-Tal, *A. Ginzberger in 1910* (WU); Kärnten Hohe Tauern, *Girtf in 1924* (W); Kärnten, Karawanken, *Girtf in 1930* (W); Vorarlberg, Bregenzerwald, E of Damuls, *H. J. v. Hattum & S. J. v. Ooststroom in 1952* (MT); Kärnten, Gailtal, *F. Höpflinger in 1949* (NDA); Tirol, Trins, Gschnitz valley, *A. Kerner, Fl. Exs. Aust.-Hung. 1272* (L, MIN, US, W); Tirol, Gerlostal, near entrance of Krummbachtal, *K. Kramer 1404* (SMU); Salzburg, Upper Pinzgan, *K. Konniger in 1936* (W); Kärnten, Klagenfurt, *Krenberger s.n.* (UC); Tirol, Kitzbühler Alps, new Bamberger Hut

to Wegscheid Guesthouse, *F. Krendl in 1969* (W); E Alps, Steiermark, SW of Kammern, *W. Möschl & H. Pittoni 71* (COLO); Salzburg, St. Johann in Pongari, *S. Müllner in 1876* (W); N Tirol, Lechtaler Alps, from Madau to Memminger Hut, *A. Polatschek in 1972* (W); Oberintal, between Schonwies & Imsterberg, *A. Polatschek in 1972* (W); Staubaier Alps, Axams, *A. Polatschek in 1975* (W); E Tirol, between Mittewald & Thal, *A. Polatschek in 1976* (W); Steiermark, Schwanberg, *E. Preissmann in 1864* (W); Kärnten, Gselsberge near Winklern, *E. Preissmann in 1880* (W); Steiermark, Grobming, *E. Preissmann in 1897* (W); N Tirol, Staubaier Alps, Neustift, Obernbergtal near Bärenbad, *M. Pull in 1971* (W); Tirol, Huben, Lienz, *J. Schneider in 1925* (W); Gailthaler Alps, Kärnten, *Tanchen in 1903* (W); Salzburg, Leogang, *J. Vetter in 1911* (W); Muhlviertal, Stratberg, *J. Wurm-Zochbauer in 1968* (W).

CZECHOSLOVAKIA—POLAND. Tatra Mts., Matadaka, *B. Kotula in 1845* (W).

DENMARK. Själland, Bögeskoven, *F. Bergesen in 1889* (MO); Själland, Valsøllile Sö, *C. Jensen in 1877* (MO); Själland, Stokkebjerg woods near Skarridso Lake, 20 mi. E of Kalundborg, *T. Leth in 1864* (DS); Jutland, SE of Vilborg, Hjermid, *T. Leth in 1873* (DS); Falster Island, *Rasmussen s.n.* (W); Silkeborg, Nesterskov, *M. ? in 1893* (W).

FINLAND. Alastaro, Kärkkäänjoki, *K. Alho in 1966* (TUR); Korpoo, Åvensor, *K. Alho & U. Laine in 1967* (TUR); Sortavala, *P. Brofeldt in 1909* (TUR); shore of Kaukjärvi Lake, opposite Talpola, *S. Cantell in 1936* (DAO); Tuktig, Salo, *G. Ekinan in 1902* (TUR); Eh, Mänttä, Mänttävuori, *P. Eloranta in 1963* (TUR); near Turku, Vihti, *A. Heikel in 1902* (TUR); Inari, Uutela, *K. Karinkanta in 1960* (DAO, TUR); Eurajoki, Kuivalahti, *I. Kause in 1963* (TUR); Rauma, Nurmisaari, *I. Kause in 1965* (TUR); Eura, Kauttua, *I. Kause & E. Seikkula in 1966* (TUR); Karhumaki, N Kumsajoki, *O. Koskinen in 1943* (TUR); Paltamo, Melalahti, *O. Kyyhkynan in 1920* (TUR); Puolanka, Salminen, *O. Kyyhknan in 1920* (TUR); Aland, Brändö, S Lappo Island, *U. Laine & J. Virtamen in 1968* (MAK, TUR, UC, W); Aland, Kökar, Karlybylandet Island, *U. Laine & J. Virtamen in 1972* (TUR); Kuusamo, Salla, near Kutsajoki R., *M. Laurilo in 1939* (H); Kuopio, *M. Lehtovuori in 1959* (TUR); Aland, Eckerö, *H. Lindberg in 1892* (W); Salmijarir, *K. Linkola in 1925* (H); Kittilä, *K. Linkola in 1925* (H); Tavastia, Sääksmäki, Ritvala, Oitti, *K. Linkola in 1932* (NCU); Kuusamo, Juuma, *N. Lounmaa in 1949* (H); Kuusamo, Paanajärvi, *H. Luther in 1933* (H); Ostrobottnia, Sotkamo, Jormasjärvi, *K. Metsävainio in 1937* (DAO, MT); Nauvo, Kasaholm, *J. Nurmi in 1963* (TUR); Etelä-Häme, Korpilahti, Rutalahti, *M. Ohenoja in 1972* (TUR); Nütty, Wüpuri, Latukkanismi, *M. Ollila in 1929* (RSA); Lammi, Untula, *J. Puro in 1955* (TUR); Säkylä, Nummioja, *H. Såltin in 1952* (TUR); S Tavasti, Kangasala, *V. Seppälä 822* (MO, UC, W); Volkeala, O. *Sikkilä in 1943* (TUR); Inari Lapnad, E shore of Lake Puolbmak, *P. Siltanen in 1964* (TUR); Kiikka, Nevo, *J. Suominen in 1960* (TUR); Punkalaidun, Kivisenoja, *J. Suominen 2407* (TUR); Tyrvää, Humaloja, *J. Suominen in 1960* (TUR); Kuusamo, Oulanka, *J. Tammisola in 1960* (TUR); Rantasalmi, Vaahersalo, *M. & P. Tsouiita in 1958* (TUR); Pohjois-Pohjanmaa, Pudasjärvi, *T. Ulvinen in 1973* (H, PH); Kuusamo, Juuma, *P. Vuori in 1958* (TUR); Porvoo, Sundö, *V. Wahlbeck in 1903* (TUR); Saarijarvi, *H. Waris in 1906* (TUR).

FRANCE. Dauphine Alps, *E. Ayasse in 1864* (UC); Isere, Grande-Chartreuse, *R. Barbezat 1323* (DAO, K, WTU); Puy-de-Dome, Mt. Dore, *P. Billiet in 1883* (LD); Haute-Pyrenees, Gavarnie, *Bordere s.n.* (G); Mende, *M. Brown s.n.* (G); Vosges, Autry, Chilimont Valley, *C. Claire 493* (DS); Haute-Savoie, forests of Goleze, *G. Delavay in 1861* (MO); Hautes-Pyrenees, Col of Bareges, *P. Estivol 9058* (G, MA, W); Hautes-Pyrenees, Cauterets, valley of Lutour, *J. Fiton 2724* (B, CAS, MT); Puy-de-Dome, Capucin, Mt. Dore, *A. Gautier in 1848* (W); Mijanes, *G. Gautier in 1894* (DS); St. Martin-Vesubie, *G. Gavelle in 1962* (MA); Vosges, Liezy, *J.-F. Jacquel in 1864* (DS); Haute-Pyrenees, Val de Gerret, between Raillere and Pont-d'Espagne, *P. Jarris 2878* (DS, MT); Savoie, forests of Belleville, Hauteluce, *E. Perrier in 1858* (UC); Vosges, Rochesson, Gerbamont, *D. Pierrat in 1869* (DAO, DS, MT); Vosges, Gerbamont, *C. Pierrey in 1865* (W); Bagneres-de-Luchon, *E. Peyron in 1892* (G); Vosges, Alsace, *B. de Retz 3439* (CAS); Hautes-Pyrenees, Cauterets, *F. Saltel in 1886* (MA); Cantal, Cirque of Falgoux, *N. Sandwith in 1950* (K); Bitche & Deaux-Ponts, *F. Schultz 32* (MO, W); Isere, St.-Mary-de-Monteymond, *M. Verlot 2878* (CAS, DS, MT); Hornschloss near Reims, *M. Veth 38* (W); Grande-Chartreuse, chemin du Sapply, *E. A. Willmott in 1860* (DAO); Boujailles, *E. A. Willmott in 1886* (DAO).

GERMANY, EAST. Thuringen, Gehlberg, *J. Bornmüller in 1912* (B); Thuringen, Masserberg, *J. Bornmüller in 1921* (B); Niesky in Lausitz, *A. Burkhardt 777* (W); Harz, Regenstein, *G. DeChalmot s.n.* (US); Neumark, Griesel, *Goleus in 1974* (B); Mecklenburg, Lubbersdorf, *K. Hahn in 1907* (B); Mark, Lythen, *Heiland in 1887* (B); Königsberg, *C. Ralintz in 1870* (PENN); Kreuzberg, *G. Schub in 1871* (DS); Elbingerode, Hohne, *R. Schube in 1913* (B); Thuringen, Leutenberg, *Wrefil in 1897* (WA).

GERMANY, WEST. Hannover, Laupark, *C. Borner in 1898* (RO); Augsburg, *Caplisch s.n.* (B); Oberbayern, near Oberaudorf, vicinity of Trisslbades, *G. Eigner & Vollman in 1902* (UC); Bayern,

Allgäuer Alps, near Obnofsdorf, *Girtf in 1916* (W); Holstein, Luebeck, *Girtf in 1931* (W); near Eschenau, *H. Glück in 1898* (UC); Bayern, Nürenburg, *H. Gluck in 1899* (MO); between Harzburg & Thorsshaus, *Heiland in 1889* (B); near Allenstein, *L. Huffen in 1936* (DAO); Oberhessen, Alsfeld, Erbenhausen, Siebenstruth, *H. Hupke in 1972* (USAS); Allgau, Freiberg, *Kuhn in 1870* (NEB); Westerwald, Lower Dreselndorf, *A. Ludwig & H. Andres 178* (W); Königsberg, Vierbrüderkrug, *C. Ralintz in 1872* (W); Bayern, Kaiserslautern, Palatin, *F. Schultz s.n.* (POM); Moelschbach & Kaiserslautern, *F. Schultz 852* (W); Hamburg, *Steetz s.n.* (PH); near Ortelsburg, *H. Steffen in 1936* (DAO); Ramsbeck, Westphalen, *J. H. Wibbe in 1863* (DAO); Bayern, Schwarzwald, Feldberg, *without collector in 1834* (NY).

HUNGARY. Szepes, Iglöfüred, *F. Filarszky, Fl. Hung. Exs. 60* (B, L, MO, MT, RO, TUR, UC, US, W, WU); Lglo (Iglo?), *Dietz in 1878* (ISC).

ITALY. Bologna, *Effaolite in 1900* (NEB); Pedemontium, Torino, Ceresole Reale, *E. Ferrari et al. 1882* (K, NEB, RO); Sappada, *Pemeri in 1934* (LD); Rio delle Finocchielle, Monte Acuto, *G. Pizzini in 1884* (RO); Appennina Modenese, near Fiumalbo, *P. Riva in 1889* (RO); Cottian Alps, Torino, *E. Rostan in 1880* (L); Forno di Zoldo, *St. Lager in 1895* (G); Bellano, Rocca di Pietore, *St. Lager in 1895* (G); Bergamo, Seriana valley, *St. Lager in 1906* (G); Appenino Lucano, near Lake Baccio, *S. Sommier in 1881* (RO).

NORWAY. Fjordane, near Fortun, ca. 5 km E of Skjoden, *C. C. Berg 70-1973* (NCU); Sør-Trøndelag, Saelbu, *F. E. Conradi in 1886* (DAO); Sogn og Fjordare, valley above Esen, near Balestrand, *R. B. Drummond 4815* (NO); Vestfold, Sande hd., Kommersøen, *J. Dyring in 1916* (COLO); Fjordane, Sogndal hd., Sogndal, *K. Faegri in 1929* (MT); Sørskjomen, head of Skjomen Fjord, *F. Fosberg 32989* (US); Viblungsnas, Romsdalen, *C. A. Gad in 1886* (WS); Polmak, Finmark, *P. Kallio in 1965* (TUR); Troms, Lyngen, *I. Kause in 1959* (TUR); Modum, *J. Lange in 1880* (MIN); Gudbrandsdalen, Ringsben, *P. Söderlund in 1904* (DAO); Ruostavand, Tromsø, *E. Taylor in 1907* (GH); Fjordane, Breim, Gravarvatnet, Egge, *O. Vasshaug in 1962* (COLO).

POLAND. Beskid Zywielki, Rezerwat Romanka, *K. Bialecka in 1965* (KRA); Brenna, Beskid Slaski, *M. Broda in 1967* (KRA); Grodziszcze Dist., Swieciany, *I. Dabkowska in 1937* (US); Wladyslawowski, *K. Drymmer in 1885* (WA); Turecki, *K. Drymmer in 1889* (WA); Wegrowski, *K. Drymmer in 1893* (WA); Gostynski, *K. Drymmer in 1895* (WA); Suprasl, *A. Ejsmonda in 1886* (WA); Rypinski, *A. Gmoud in 1885* (WA); Bystrzyca Kłodzka, Spalona, Slask Dolmy, *S. Gołowin, Fl. Silesia Exs. 160* (DAO, TUR, W, WA); Lukowski, *Kazimierz in 1874* (WA); Warszawa, *Kazimierz in 1877* (WA); Kielce Dist., Bukowa gora near Klonow, *K. Kaznowski in 1926* (POM); Białowieza National Park, part of the Puszcza Biolowieska, primeval forest on the Russian border, *P. Ketner 350* (KYO, SHIN); Pieniny Mts., Nowy Targ Dist., Kroscienko, *I. Kucowa 239* (COLO, KRA, KYO, MO, NCU, PH, UBC, UC, WA, WTU); Majdan, *F. Kwiecinski 788* (WA); Sudetic Mts., Sudetica, Winkelsdork, *F. Lanück in 1925* (MSTR); Tuchow, *Z. Lapczynski in 1874* (WA); Tatry Mts., *Z. Lapczynski in 1880* (WA); Pomorze Zach, Chojnice, *S. Lisowski et al. in 1968* (KRA); W Carpathians, Tatri, Bobrowiec nad Polana Chocholowska, *J. Madalski et al., Pl. Pol. Exs. 351* (DS, KRA, KYO, L, MO, MT, US, WA); Pieniny Mts., Nowy Targ Dist., *H. Piekos in 1970* (SMU); Kotlina Sandomierska, Wola Zarczycka, *Z. Raciborski 672* (KRA, WA); Kotlina Sandomierska, Wola Zarczycka, Lezajskiem, *M. R. Rosling Polskie in 1909* (KYO); Gory Swietkrzyskie, *Schuabel s.n.* (WA); E Prussia, Kreis Goldap, Borvalker Forest, *R. Schultz 344* (CAS); Dobrznska, *H. Talewski in 1890* (WA); Wadowice Dist., Lanckorona, *J. Trela, Pl. Pol. Exs. 351* (DS, KRA, KYO, L, MO, MT, WA); E Schlesien, *J. Vetter in 1908* (W).

ROMANIA. Balcani Comm., Frumoasa, *N. Barabas, Fl. Exs. Bacov. 428* (TUR); Bucovina, Piatra Liboa, *D. Herbich s.n.* (W); Sinaia, *Loitlesberger in 1897* (W, WU); Moldavia, near Cirlibaba, *D. Mititelu et al. 252* (WA); Transsilvania, Odorhei Dist., above Corund, *E. Nyarady, Fl. Rom. Exs. 1297* (MO, RO, US, W, WA).

SPAIN. Navarra, Roncesvalles, *L. Nee in 1786* (MA); Pirineo, entrance to Caldes de Bohi & Estang de Cavallers, *without collector in 1944* (MA).

SWEDEN. Södermanland, Musko socken, Gullboda, *E. Asplund in 1924* (MO); Närke, Hidinge, *E. Asplund in 1925* (UC); Södermanland, Grödinge, Tegelvreten, *E. Asplund in 1930* (CAS, MO, RM); Östergötland, Gryt, Väggön, *E. Asplund in 1945* (RO); Södermanland, Paroecia, Sorunda, Villkulla, *E. Asplund, Pl. Suec. Exs. 1223* (COLO, DAO, MT, MTJB, NCU, RSA, W); Dalarne, Norrbärke, Dagkarlsboberget, *R. Bergland in 1964* (SMU, TUR); Ångerwauland, N of Fjardbotten Skog, *E. Evers in 1964* (MAK); Västmanland, Fagersta, *E. Folkesson in 1940* (MO); Ångermanland, Österåsens Sanatorium, *H. Fries in 1903* (MT); Värmland, Råda, *H. A. Froding in 1895* (MT); Småland, Ljongarum, Sanna, *Fr. Hagstrom in 1890* (DAO); Skåne, Ivetofta, Bromölla, *C. Hammarlund in 1958* (COLO); Västergötland, Östad, Ramdalen, *T. E. Hasselrot in 1952* (RO); Madelpad, Singo,

G. Hjort in 1906 (W); Östergötland, Omberg, *K. Holm in 1924* (WTU); Madelpad, Timrå, *K. Holm in 1953* (SMU); Vermelandia, Vidan, *A. Hulphers in 1899* (MIN); Avesta, Dalecarli, *C. Indebetou in 1889* (MA); Halleburg, *K. Kahne in 1910* (MIN); Närke, Hallsberg, Skäleklint, *G. Kjellmert in 1942* (UC); Skåne, Stenestad, *H. Lanander in 1903* (MO); Helsingland, Färila Parish, Skyte, *G. Lidman in 1933* (RM); Östergötland, Omberg, *C. O. U. Montelin in 1878* (ISC); Gunnebo, *H. Ohlemann in 1890* (MA); Uppland, Ljusterö Parish, Östra Lagnö, *C. Ringenson in 1918* (W); Uppland, Ljusterö, Östra Lagnö, *C. Ringenson in 1923* (WS); Västergötland, Borås, Almenäs, *C. Sandberg in 1938* (MT); Ångermanland, Överlännäs, *G. Söderholm in 1909* (SMU); Västergötland, Ugglum, *S. Vallquist in 1911* (DAO); Värmland, *B. Weiner in 1888* (MTJB); Skåne, Ängelholm, *E. Wieslander in 1970* (VDB).

SWITZERLAND. Graubunden, Prätigau, *H. Berger in 1913* (B); Lucomagno Mt., Medels & St. Maria Valleys, *R. & A. Keller in 1900* (Z); Tarasp, *Killias in 1870* (Z); Prätigau, Arosa, *J. Macfarlane in 1906* (MO, PENN, US); Vaud, Bex, *Schleicher s.n.* (UC).

UNITED KINGDOM: ENGLAND. Westmorland, Knock Fell, Moor House Reserve, *A. Eddy in 1961* (DS); Westmorland, Knock Ore Gill Head, *A. Proctor in 1964* (DS); Westmorland, Glencoyne Woods, Ullswater, *P. Raven 16222* (DS). SCOTLAND. Arran Island, Brodick, *Lenox? in 1885* (DS); Easterness, Suidhe, Kincraig, *M. McCallum-Webster 16625* (MO). WALES. Merioneth, Penant Dyfi, *P. H. Raven & W. Condry 16294* (DS).

YUGOSLAVIA. Kroatia, Plitvice, *A. Ginzberger in 1909* (WU).

U.S.S.R.

AZERBAIJAN S.S.R. Caucasus Mts., Balkovia, Agaschtan, *E. & N. Busch in 1925* (S); Caucasus Mts., Kuba Dist., between Leze & Mt. Kyzyl-kaja, *I. Karjagin in 1935* (NY, UC). BELORUSSIAN S.S.R. Mogilev Prov., between Mogilev & Borysthenen, *N. Downer 1862* (MW); Minsk Prov., Iqumensk Dist., Zhornovska, 4 km W of Lapiczi, *O. Polianskaja in 1924* (MW); Veliki Berezny, Lyuta, *A. K. Skvortsov in 1968* (MO); Brest, *A. K. Skvortsov in 1974* (MO). ESTONIAN S.S.R. Wesenberg, Vezo, *S. S. Ganeskin in 1913* (MW); Parnumaa, Voltveti, *O. Kyyhkynen & K. Linkola in 1924* (TUR); Tartto, Vasula, *O. Kyyhkynen & K. Linkola in 1924* (TUR); Krestovskiy Island, *D. E. Regel in 1866* (L, MIN, NDG, W). GEORGIAN S.S.R. Osetiya, between Tkue & Kosekha, *A. H. & V. F. Brotherus 343a* (BM), *342* (BM, H; *C.* × *intermedia* and *C. lutetiana* subsp. *lutetiana* also part of this collection); Mt. Kazbek, *A. H. & V. F. Brotherus 343* (H); Caucasus Mts., Ratcha Mts., *A. K. Skvortsov in 1976* (MO). KAZAKH S.S.R. Ust-Kamenogorsk Prov., Bolschenarimskoje Dist., Narimski, *V. N. Voroshilov 4183* (MHA). LATVIAN S.S.R. Curonia (Kurland), Papenhof & Kalnischke, *P. Lakschewitz 9669* (MO); at the Dvina R., near Koknese, *P. Lakschewitz 7498* (MO). LITHUANIAN S.S.R. Kaunas, *B. Hryniewiecki in 1899* (WA); Kupishkis, *A. Kranckiewicz in 1939* (WA); Shamajski, Shilueny, *P. Maziljascaite in 1958* (MW); Vilnius, *J. Schnell s.n.* (WA); Minojty, Lida Dist., *T. Symonowiczowna 434* (KRA, W, WA, WU). MOLDAVIAN S.S.R. Suceava Dist., *D. Mitetelu et al., Fl. Moldavia Exs. 252* (TUR). RUSSIAN S.F.S.R. Khabarovsk Prov., at the Taykan R., *M. A. Akhmet'ev in 1961* (MHA); Leningrad Prov. Kingisepp Dist., Narovski, Kurgolovski, *A. G. Borisova 698* (MW); Sachalin, near Kussunai, *Brylkin in 1860* (K, UPS); Pskov Prov., Velikolutzski Dist., Vladykino, *A. Bulevkina & N. Ikonnikov-Galitzky in 1921* (MW); Kuban Prov., Teberda R. valley, mouth of Amananda R., *N. A. Busch in 1896* (NY, W); Caucasus Mts., Kuban Prov., *E. Busch in 1909* (DS); Novesiverskaya, vicinity of Leningrad, *Chermjakoskya 73* (DAO); Amur Prov., divide between Nora & Mamyra Rivers, *V. S. Dokturovsky 1326* (S); Sachalin, Moneron (Kaibato) Island, *E. Egorova 2557* (MHA); Sachalin, Makharov Dist., Gornaya, *E. Egorova & L. Koltschanova 2879* (MHA); Sachalin, Smirnykh, *E. Egorova & A. Tschernyayeva 3639* (MHA); Kamtschatka, vicinity of Eligovo, *E. Egorova & V. Voroshilov 9776* (MHA); Kurbulik, middle part of Lake Baikal, *S. J. Enander in 1913* (S); Transbaical, Kyrmyko, *S. J. Enander in 1913* (S); Kamtschatka, Savoiko, *W. Eyerdam in 1928* (GH, MICH, MO, NY, US); Sachalin, Takinosawa, *U. Faurie s.n.* (KYO); Sachalin forests of Vladimirov, *U. Faurie 423* (BM, KYO, P); Viatke Prov., Bassein, Malmyzh, *A. Fokin 142* (MW); Leningrad Prov., Shlieselburg Dist., Neva R., Peski, *S. S. Ganeshin in 1915* (MW); Moscow Prov., Losinojostrow, *W. Grigoryev 515* (G, W, WA, WU); Irkutsk Dist., near Kukunut, *M. A. Hilova 164* (H); Sachalin, Mt. Tosso, *N. Hiratsuka in 1927* (SAP, TI); Sachalin, Yuzhnosakhalinsk ("Toyohara"), *M. Honda & Y. Kimura in 1940* (TI); Kamtchatka, S shore of Avacha Bay, Bogatyrjovka, *E. Hulten 456* (S), *E. Hulten 472* (CM, S); Kamtchatka, Golygina village, *E. Hulten 2745* (S); Middle Ural, Michaelovski tract, *K. I. Igorshina in 1939* (MW); Tverj Prov., 3 km W of Pavlovskaja, *A. Iljinskin in 1927* (MW); Zejskaja Pristan at the Zea R., *F. Karo 283* (BM, E, P); Khabarovsk Prov., Mamyn, *Karpenko 21* (MHA); Novgorod Prov., near Novgorod, *A. Khokhryakov in 1966* (MO); Yakutiya Dist., Aldan, Ajkokit, *A. Khokhryakov & M. Mazurenko in 1968* (MHA); Novgorod Prov., Borovicz Dist., Msta R. valley, *V. Komarov in 1915* (MW); Sachalin, Moneron ("Kaibato") Island, *S. Komatsu in 1915* (TI); Leningrad, banks of Neva R., *F. Kornicke in 1857* (S); Kasan, Yadrin, *S. Korzchinsky in 1884* (ISC); Kasan Prov., Zarewokokschaisk Dist., between Negodajevo & Abasnur, *S. Korzchin-*

sky in 1885 (MW); Krasnojarsk Prov., Chakarija Dist., Jaschtip, Abaza, *E. Kravtsova 77* (MHA); Tobolsk Prov. & Dist., *P. N. Krylov & D. Sergievskaya in 1927* (NY); Tobolsk Prov., Tobolsk, *P. N. Krylov & D. Sier s.n.* (NY); Baschkin Prov., Birsk, *S. E. Kucherovskaja 843* (MW); Khabarovsk, Bolon-Odshalense, Amur, *I. W. Kusnezow 382* (DS); Leningrad Prov., Luga Dist., Staritza R., *N. Lavitch 94* (S); S Kamtchatka, Nikolajevsk, Podpruginski, *R. Malaise in 1928* (S); S Kamtchatka, Lake Assabatche, *R. Malaise 490* (S); central Kamtchatka, Shtchapina, *R. Malaise 3477b* (GH, S); Makarov Dist., vicinity of Zaozernoye, *E. Mikhalchenkova 1198* (MHA); Lipeckyi, near Voranova, *T. Mojevikina in 1967* (DAO); Vladimir Prov., Melenkovski, between Adina & Sykova, *M. I. Nasarow 1653* (MW); Khabarovsk Prov., Sovetskaya Dist., Gavan, Tulutchi, *A. Nechayer 159* (MHA); Smolensk Prov., Dorogobuzhski, Batischevo, Engelhardt Expt. Sta., *O. Neumark 53* (MO, MW); around Peterbourg, *M. Patrin s.n.* (G); Pskov Prov., Ostro Dist., Dubovsk, *N. Puring in 1895* (MW); Moscow, *A. P. in 1888* (WU); Yaroslav Prov., Pybinsk Dist., Yremetien, Volga R., *I. I. Sapozhnikova in 1924* (MW); Olonez Prov., Petrogavodsk Dist., Sandal Lake, *V. P. Savicz 000944* (MW); N Dvinsk Prov., Kotles Dist., Gorodok, *E. Selevanova in 1927* (MW); Khabarovsk Prov., Bogoradskaja, *N. & V. Shaga 73* (MHA); S Urals near Miass, *A. K. Skvortsov in 1950* (MO); Primorski Prov., Sutschan, Uslpachanovka, *A. K. Skvortsov in 1967* (MO); Altai Mts., Labed R. near Biya, *A. K. Skvortsov in 1971* (MO); Altai Mts., N end of Teletskoye Lake, *A. K. Skvortsov in 1971* (MO); Moscow Prov., Mozhaisk Dist., 152 km hwy Moscow–Minsk, *A. K. Skvortsov in 1972* (MO); Caucasus Mts., Kabardino-Balkaria, Cheghem, *A. K. Skvortsov in 1976* (MO); Laatokan Karjala, Sortavala, Malkynvuori, *N. Soyrinki in 1929* (UBC); Pensa Prov., Pensa Dist., Arbekovo, Dvoinigory Mts., *I. I. Sprygin in 1906* (MW); Moneron Island, *Stepanova 230* (MHA); Vladimir Prov., Gus-Rustalny region, between Grasnoje Ecko & Dubasova, *V. Tihomirov et al. 7661* (MW); Sachalin, Anbetsu, *Y. Tokunaga & K. Kawai in 1929* (SAP); S Ural, vicinity of Miass, Ilmen Mts., *L. Tyulina in 1927* (MW); Samarski Prov., Bohilovski Forest, bank of Erika R., *A. Uranov et al. 1596* (MW); Konda, Leusch, *E. Vainio in 1880* (TUR); Kamtchatka, Karaginskiy Island, *V. N. Voroshilov et al. in 1969* (MHA); Primorski Prov., Svetlaya, *V. N. Voroshilov 517* (MHA); Khabarovsk Prov., near Komsomolsk, *V. N. Voroshilov 2073* (MO); Khabarovsk Prov., near Komsomolsk, *V. N. Voroshilov 9073* (MHA, MO); Sachalin, Poronajsk Dist., *V. N. Voroshilov 11500* (MHA); Leningrad Prov., Luga Dist., E shore Lake Sjaberskoja, *N. Winter 5828* (MW); Irkutsk, Okaensi-angarense, *without further data* (UC); Tambov Prov., Sparsskiy, Zubova-Poljana, *without collector in 1884* (MW). UKRAINIAN S.S.R. Czernigov Prov., *Borysov in 1859* (MW); near Thytomir, *Degener 3497* (NY); Bukovina, Pojana-Stampi, Mt. Ascutiti, *J. Dörfler in 1889* (WU); Zarkapatskaja Prov., Sujaljavska, Obava village, *K. I. Igorshina in 1949* (MW); Kiev, near Woskrejenskaja, *I. Schmawlhausen in 1892* (MW); Verkhovina Dist., near Burkut, Cheremosh valley, *A. K. Skvortsov in 1968* (MO); Nizhegorodski Prov., Gorodski Dist., Kalushki, *S. Stankov et al. in 1927* (MW); Ivano-frankovski Prov., Carpat Preserve, *V. M. Vinogradova in 1977* (MW).

KURILE ISLANDS. Some of the Kurile Islands are claimed by Japan but occupied by the Soviet Union. Collections from this chain of islands are here listed separately. Kunashiri Island, *L. Alexeeva et al. 5915* (MHA); Onekotan Island, Shiomiura, *S. Berman 198* (GH, S); extreme E Shikotan Island, *B. Butovski in 1968* (MHA); Onekotan Island, *A. Chernyaeva in 1962* (MHA); Shumshu Island, *E. Egorova & E. Sharamova 4183* (MHA); Kunashiri Island, Nikishoro, *K. Ito in 1939* (SAP); Paramushir, at Shirakawa, *Y. Kudo in 1920* (TUS); Kunashiri Island, Chishima, *Y. Matsumura in 1930* (KYO); Shikotan Island, Mt. Shakotan-yama, *J. Ohwi 523* (KYO); Shikotan Island, Umanose, *J. Ohwi in 1931* (KYO); Shumshu Island, *J. Ohwi & R. Yoshii 252* (KYO); Alide Island, Minamiura, *J. Ohwi & R. Yoshii 5832* (KYO); Paramushir Island, *J. Ohwi & R. Yoshii 6128* (KYO); Shikotan Island, *E. Sharamova 3999* (MHA); Shikotan Island, Anama, *G. Tanaka & K. Miyabe in 1910* (SAP); Urup Island, Hayakawa valley near Onsenzaki, *M. Tatewaki in 1927* (SAP); Kunashiri Island, *V. N. Voroshilov 10239, 10421* (MHA); Iturup Island, *V. N. Voroshilov 10776* (MHA); Shumshu Island, *K. Yendo in 1903* (TI).

ASIA

CHINA. HEBEI: Hsiaowutai-shan, *C. W. Wang s.n.* (PE). HEILONGJIANG: Dai-lin, *A. Baranov et al. 6070* (LE). JILIN: Lialugo, *T. U. Liou 3534* (LE); Szeping (Ssu-p'ing-chieh), Mt. Chang-pai, *C. Y. Wu & I. L. Chou 1719* (PE). LIAONING: Between the villages of Liubzjadantzy & Sipindze, *Y. L. Chang et al. 314* (LE); between the villages of Leuanihe & Liubzjadantzy, *S. K. Wang & Y. L. Chou 230* (LE). "MANCHURIA": Teingan Dist., near village of Teingan, *D. Litvinov 636* LE).

JAPAN. HOKKAIDO: Iburi, Tomakomai Experimental Forest of Hokkaido Univ., *D. E. Boufford & E. W. Wood 19660* (CM, KYO, MO); Abashiri, Abashiri-gun, Tsubetsu-cho, NW end of Lake Chimikeppu-ko, *D. E. Boufford & E. W. Wood 19786* (KYO, MO); Rishiri Island, Higashirishiri-cho, Omobetsu-zawa, *D. E. Boufford & E. W. Wood 19823* (KYO, MO); Kawakami, border of Nakagawa-cho & Otoineppu-mura on hwy 40, *D. E. Boufford & E. W. Wood 19833* (KYO, MHA, MO); Otaru, *U. Faurie 1184* (K, KYO, MO, P); Hidaka, Mt. Apoi, *H. Hara in 1933* (ORE); Ishikari, Sorachi-gun,

Minamifurano-mura, Mt. Tomamu, *M. Hiroe 6944* (TNS); Kushiro, Mt. Meakan, *S. Kitamura in 1956* (KYO); Oshima, Gamushi, *Y. Kudo in 1917* (TUS); Kitami, Rishiri, *Y. Kudo in 1916* (TUS); Nemuro, Shibetsu, *K. Miyabe in 1884* (GH); Asahikawa, Kamui-kotan, *S. Okamoto 1433* (KYO); Rebun Island, Rebun-gun, Kabuka-mura, Shireto-ko from Momoiwa, *T. Shimizu 1505* (SHIN); Ishikari, Nopporo, *T. Tanaka 243* (BM, NY, P, S, US); Mt. Daisetsu, Yukomanbetsu-Tenninkyo, *T. Yamazaki 747* (NCU, TI). HONSHU: AICHI PREFECTURE, Mt. Dando, Uratani, *K. Torii in 1960* (KANA); AKITA PREFECTURE, Kita-akita-gun, Mt. Moriyoshi-yama, *S. Kurosawa in 1959* (TI); Oga Peninsula, Motoyama, *R. Mochizuki 583* (KANA); AOMORI PREFECTURE (Mutsu), Mt. Hakkoda, *K. Okamoto 777* (A, B, BH, BM, DAO, E, G, H, K, KAG, KANA, KYO, MAK, MICH, MO, MT, MTJB, NA, NY, S, TI, TNS, TUS, UC, UPS, US, WTU); Kita-tsugaru-gun, Odomari, *K. Hosoi in 1953* (KANA); FUKUI PREFECTURE, Mt. Arashima-dake, Oono city, *G. Murata & T. Shimizu 476* (KYO); FUKUSHIMA PREFECTURE, Mt. Iide, *T. Saito T108* (TI); GIFU PREFECTURE, Masuda-gun, Osaka, *M. Mizushima in 1954* (MAK); GUNMA PREFECTURE (Kotsuke), Doai, *J. Ohwi & T. Koyama 278* (A, AA, B, BH, BM, DAO, E, G, H, K, KAG, KANA, KYO, L, MICH, MO, MT, MTJB, NA, NY, P, S, SAP, TI, TNS, TUS, UPS, US, W, WTU); Tone-gun, Katashina-mura, E side of Marunuma, *M. Ono & S. Kobayashi in 1965* (KYO, MAK, TUS); HYOGO PREFECTURE, Yabu-gun, Sekinomiya-cho, Mt. Hyonosen, *D. E. Boufford et al. 19559* (CM, G, GH, KYO, MHA, MO, PE); ISHIKAWA PREFECTURE, Hakusan, *G. Masamune 7127* (KANA); IWATE PREFECTURE, Hienuki-gun, Odagoe in Mt. Hayachine, *D. Shimidzu 12481* (TNS); KANAGAWA PREFECTURE, Hakone, Kamiyama, *M. Mizushima in 1961* (MAK); MIE PREFECTURE, Iina-gun, Myojin-daira near Mt. Kumini, *K. Seto 9865* (OSA); NAGANO PREFECTURE, en route from the summit of Mt. Choga-dake to Mitsumata, *D. E. Boufford et al. 19885* (KYO, MHA, MO); from Akagawara to Kitazawa-toge, Mt. Senjo-dake, *K. Iwatsuki et al. 116* (KYO); Kiso-gun, Mt. Ontake near Miure Dam, *M. Mizushima 10823* (S, TI); Mt. Karamatsu, *S. Okamoto in 1935* (KYO, SHIN); NARA PREFECTURE, Yoshino-gun, Mt. Omine, *T. Shimizu 4368* (S), *T. Shimizu 4408* (SHIN); NIIGATA PREFECTURE (Uzen), Nishiokitama-gun, Mt. Iide, *T. Makino* MAK *6911* (S); SAITAMA PREFECTURE, Chichibu, Mt. Kobushi-dake, *K. Hisauchi 1639* (TI); SHIZUOKA PREFECTURE, S slope of Mt. Fuji-san, Omotefujinigome, *G. Murata et al. 33934* (KYO, MO); TOCHIGI PREFECTURE, Nikko city, road to Kirikomi Lake, *M. Ono & S. Kobayashi in 1963* (CAS, S, UC, US); TOTTORI PREFECTURE (Hoki), Mt. Daisen, *G. Murata in 1958* (KYO); TOYAMA PREFECTURE, Shimoshinkawa-gun, Asahi-machi, Kitamata, Mt. Iburi, *H. Kanai in 1958* (TI); WAKAYAMA PREFECTURE, Itsu-gun, Koya-cho, Mt. Koya-san, *without collector in 1912* (MAK 117703); YAMAGATA PREFECTURE, Nishiokitama-gun, Mt. Iide, *T. Makino in 1904* (S); Mt. Chokai-san, *S. Ishizuka 111* (TI); YAMANASHI PREFECTURE, W side of Mt. Fuji-san, *H. Ohba 69826* (TI). KYUSHU: FUKUOKA PREFECTURE (Busen), Togawa-gun, Mt. Eihiko, *T. Makino in 1906* (S); Tagawa-gun, Mt. Hiko-san, *T. Makino in 1906*, MAK *6901* (KAG, KYO, MAK, S); KAGOSHIMA PREFECTURE, Yakushima, Mt. Takatsuka, *S. Hatusima 14750* (KAG); Yakushima, Yaku-cho, near the summit of Mt. Miyonoura, *G. Murata & H. Tabata 454* (KYO), *M. Tagawa 1957* (KYO); KUMAMOTO PREFECTURE, Gokanosho, Mt. Kamifukune, *S. Hatusima & S. Sako 27086* (KAG, MAK); MIYAZAKI PREFECTURE, Hori & Mt. Okue, *S. Hatusima & S. Sako 24912* (KAG, KYO, MAK); Mt. Shiraiwa, *S. Hatusima & S. Sako 26330* (KAG); NAGASAKI PREFECTURE, Nagasaki, Shimabara, *C. Maximowicz in 1863* (BM, K, LE, P); OITA PREFECTURE, Mt. Kuju, Hokein, *T. Naito in 1922* (KAG); Mt. Sobo-san, *T. Naito in 1923* (KAG). SHIKOKU: EHIME PREFECTURE, Kamifua-gun, Omogo, *T. Makino in 1931* (MAK); KOCHI PREFECTURE, Kami-gun, Mt. Shiraga, *T. Makino in 1934*, MAK *6900* (KANA, MAK, S); Nanokawa, *K. Watanabe in 1884* (TI); TOKUSHIMA PREFECTURE, Mt. Tsurugi-san, *H. Kimura in 1950* (TI); Omogo, Mt. Ishizuchi, *T. Makino in 1931*, MAK *6914* (KAG, MAK, S).

KOREA, NORTH. Hamgyong-Pukto, *M. Furumi 428* (TI); Kaema-Kowon (Prov. Kannan, Kaima Plateau), *S. Kitamura in 1932* (KYO, MAK, MICH, TNS); Handae-Ri (Pyangkan-do, Handaeli), *T. Nakai 15600* (TI); Hamgyong-Namdo, S foot of Mt. Chapek-Bong, *T. Nakai 15601* (TI); Kankyo-nando, Cho-shing Co., Shing Katsu-men, *N. Namura in 1934* (KYO); Rekketsu-sui R., *J. Ohwi 2960* (BH, KYO, UPS); Hamkyongnan-do, *Y. Oikuma 372* (TI); Kyanwonpuk-do, Mt. Gumgang-san, *T. Uchiyama in 1902* (TI).

KOREA, SOUTH. Cheju-do Island (Quelpaert Island), *Chung In-cho 3898, 3899* (MICH); Cheju-do ("In forests Quelpaert"), *U. Faurie 1834* (KYO); Cheju-do (Quelpaert), *T. Mori 150* (TI); Kyongsangnam-do, Mt. Chii, *J. Mori 239* (TI); Kyongsangnam-do, Mt. Chii ("Mt. Jiili-san"), *T. Nakai in 1913* (TI); S Chulla Prov., Mt. Chii ("Chirisan"), *Mrs. R. K. Smith in 1934* (GH); Cheju-do Island ("In forests Quelpaert"), *E. Taquet 186* (KYO); Cheju-do, Hallai-san, *E. Taquet 832* (LE); Cheju-do, N in sylvis, *E. Taquet 4258* (G); Cheju-do, *E. Taquet 4298* (LE); Cheju-do Island ("Isl. Saisyu"), Kanra-san, *K. Uno 2598, 23754* (GH); Cheju-do Island ("Island of Sai-shu-to"), *without further data* (KYO). KOREA, UNKNOWN LOCALITIES: Kanhoku, Mt. Tosho, *G. Koidzumi in 1933* (MICH); Kankyohokudo, Minami-kegoku-san, *T. Saito 692* (KYO).

MONGOLIA. Hentiyn Nuruu Mts., bank of Minjiyn Gol R. ("Kentei Mts., Mensa R."), *N. & V. Ikonnikov-Galitzky 3201* (S, UC), *3274* (LE, UC); Hentiyn Nuruu Mts., at the Yoroo Gol R. ("Kentei

Mts. at the Tola R."), *N. & V. Ikonnikov-Galitzky 3301* (NY, S, UC); bank of the Minjiyn Gol R. above Uber-Katanse R., *N. & V. Ikonnikov-Galitzky 3301* (NY, POM); Rican R., *P. Mihno in 1924* (LE).

TURKEY. Coruh, Savval Tepe, above Margul, *P. H. Davis & I. C. Hodge 32258* (BM, K); Pontus region, Ciganadagh, *P. Sintenis 1370* (LD, WU); Pontus, Lumila, *P. Sintenis 1456* (LD).

Circaea alpina subsp. *alpina* is by far the most wide ranging of the species of *Circaea*. Except for size, it is remarkably uniform throughout its entire range both morphologically and in ecological preferences. Size differences appear to be primarily due to local conditions of the habitat; high elevation and northern plants tending to be often considerably reduced in stature.

Circaea alpina subsp. *alpina* appears to be most closely related to subsp. *micrantha*, based on morphological characters, and is sometimes separated from that subspecies with difficulty. *Circaea alpina* subsp. *micrantha* grows at higher elevations (3,000–5,000 m) than subsp. *alpina* and is restricted to the high mountains in the Himalayan region and western and southwestern China. It differs from *C. alpina* subsp. *alpina* in having more coarsely dentate or serrate leaves that are usually more slender and tapering than in subsp. *alpina*. The petals in subsp. *micrantha* are often emarginate or only barely notched, the notch being 0.3 mm deep or less and less than one fifth the length of the petal. In *C. alpina* subsp. *alpina* the notch is 0.3 mm or more deep and more than one quarter the length of the petal. At anthesis the ovaries of *C. alpina* subsp. *micrantha* are glabrous, the uncinate hairs developing after the shedding of the floral tube, while in subsp. *alpina* minute hairs are present on the ovary at anthesis. Care should be taken in using the last character, however, since the numerous bundles of raphide crystals in the outer ovary walls often appear under magnification to be minute appressed hairs. *Circaea alpina* subsp. *micrantha* tends also to have the axis of the inflorescence more densely glandular-pubescent than in the majority of plants of subsp. *alpina*.

In western North America *Circaea alpina* subsp. *alpina* comes into contact with subsp. *pacifica*. Throughout much of their ranges these two subspecies remain distinct but intermediate plants occur in the Rocky Mountains, in the state of Washington, and in British Columbia. *Circaea alpina* subsp. *pacifica*, commonly a more robust plant than subsp. *alpina*, has leaves that are subentire or with only minute teeth and that are most commonly rounded at the base. The stem of subsp. *pacifica* is also coarser and bears sparse to dense falcately recurved hairs. In cases where it is difficult to assign plants to either *C. alpina* subsp. *alpina* or subsp. *pacifica* using size and leaf characters, I have tended to base my decisions on this pubescence character, calling plants with at least a few recurved hairs on the stem subsp. *pacifica* and those that are totally glabrous subsp. *alpina*.

Plants that appear to be intermediates between *Circaea alpina* subsp. *alpina* and subsp. *pacifica* set a full complement of fruits, which appear to be completely fertile. The lack of field observations and the often poor label data on specimens make it difficult to distinguish ecological differences between these two subspecies but what information is available seems to indicate that subsp. *pacifica* may often be somewhat weedy, at least near the Pacific coast where it appears in hedges and in gardens. Relatively few herbarium sheets with mixed collections of *C. alpina* subspp. *alpina* and *pacifica* exist, indicating either that the plants

are very distinct when growing together and easily separated in the field or that they rarely grow intermixed. One particularly well distributed example, however, is that of *Thompson 14701* from Big Four Inn, Snohomish County, Washington, which includes plants of both subspecies on most sheets.

In Japan, northeastern China, Far Eastern U.S.S.R., Lake Baikal, the Altai region, and in the Caucasus Mountains, *Circaea alpina* subsp. *alpina* comes in contact with subsp. *caulescens*. *Circaea alpina* subsp. *caulescens* differs from subsp. *alpina* in having larger flowers that open after elongation of the raceme axis and are held perpendicular to it, the absence of bracteoles in most instances, thicker leaves which are often pubescent above, and coarser stems that are pubescent with short, falcately recurved hairs. The stems of subsp. *caulescens* usually remain unflattened after pressing. Skvortsov (1970) has stated that he has not observed intermediates between these subspecies in any of the localities in the U.S.S.R. that he was able to observe even though they often grow near each other. In Japan, in Nagano Prefecture in central Honshu, both subspecies grow in seemingly identical habitats on adjacent moss-covered rocks at Tobira-onsen without the presence of intermediates. Both subspecies also occur on Mt. Chausu-yama, also in Nagano Prefecture, but there *C. alpina* subsp. *alpina* is restricted to the conifer forests above 1,500 m while subsp. *caulescens* is in deciduous or mixed forests at elevations usually below 1,300 m. At Lake Chimikeppu-ko in Hokkaido both subspecies are present at the same elevation but with *C. alpina* subsp. *alpina* abundant and restricted to wet moss-covered logs and rocks and to wet seepages in deep shade, while subsp. *caulescens* is scarcer and grows in drier soil (not in moss) and is restricted to woodland margins. In neither of these locations were interemdiates found. However, in southern Hokkadio at the Tomakomai Experimental Forest of Hokkaido University, a situation occurs where the majority of plants of *Circaea alpina* are intermediate between subspp. *alpina* and *caulescens*. There, both subspecies are relatively scarce, *C. alpina* subsp. *alpina* being restricted to deep shade or moss-covered rocks and logs and subsp. *caulescens* in more open areas in loose soils and as an epiphyte on the trunks of trees. The abundant intermediates are in thin second growth forests in low depressions on the forest floor and on well decayed, but not moss-covered, logs. The intermediates are fully fertile with abundant fruit set.

Other plants that appear to be intermediate between *C. alpina* subsp. *alpina* and subsp. *caulescens* are: Korea, Hamkyongnan-do, S foot of Chapek Bong, 15 August 1935, *T. Nakai 15601*, TI (this sheet represents a mixed collection of subsp. *alpina* and subsp. *caulescens* that Nakai called all subsp. *caulescens* var. *robusta*; the plants grade smoothly into each other in all characters); Korea, Keishonan-do, Mt. Chii-san, 8 August 1938, *K. Uno 23366*, GH (these plants have the thin, sharp-toothed leaves, flattened stems and very flattened petioles of subsp. *alpina* but lack bracteoles and have the stem pubescence and open inflorescence of subsp. *caulescens*). In addition, several other collections representing varying degrees of intermediacy occur.

Despite the fact that *Circaea alpina* is predominantly self-pollinating, during favorable weather the flowers are visited by numerous small insects, mostly syrphid flies and halictid bees. The chief syrphid visitors in North America are *Toxomerus geminatus* (Say) and *Melanostoma mellinum* (Linnaeus) while the

halictid visitors consist of diverse species. Rare visits by bumblebees and butterflies also occur but these visitors usually fly on quickly after visiting a single inflorescence. Both *T. geminatus* and *M. mellinum* are important visitors to the flowers of *Circaea lutetiana* subsp. *canadensis*.

Circaea alpina subsp. *alpina* is often confused with the hybrids formed between it and other species of the genus. Although in most cases the hybrids are more robust, morphologically they tend to resemble *C. alpina* subsp. *alpina* more closely than they do the other parental species. This is most evident in the shape and toothing of the leaves and in the succulent nature of the stem. All known hybrids involving *C. alpina* subsp. *alpina* have as the second parent species that have the nectary protruding as a fleshy disc above the opening of the floral tube, bilocular fruits, and the flowers held on pedicels that are perpendicular to the raceme axis. In *C. alpina* the nectary is always well within the floral tube, the fruit is unilocular, and the flowers are held on erect or ascending pedicels in clusters at the apex of the racemes. The hybrids always exhibit a low, but exserted, nectar-secreting disc, abortive fruits, and flowers held in an intermediate position between that of the parents or on pedicels held perpendicular to the raceme axis. The known hybrids involving *C. alpina* subsp. *alpina* include as the second parent *C. erubescens* and all subspecies of *C. lutetiana*. Hybrids between *C. alpina* subsp. *alpina* and *C. cordata* and *C. mollis* should be sought in the field. *Circaea alpina* subsp. *alpina* and *C. cordata* grow in close proximity on Hokkaido in Japan but no clear hybrids between them have been detected.

7f. Circaea alpina L. subsp. **micrantha** (Skvortsov) Boufford stat. nov. Based on *Circaea micrantha* Skvortsov, Bull. Glavn. Bot. Sada 103: 36. 1977.—FIG. 22.

Plants 0.4–2.5 dm tall. The stem glabrous or minutely pubescent, very rarely densely pubescent, with soft, short, falcately recurved hairs 0.1–0.2 mm long; the petioles glabrous or with sparse hairs as on the stem but upwardly curved; the leaves glabrous or pubescent along the veins and occasionally over the entire surface above with short falcate hairs, sometimes also with strigillose hairs intermixed; the axis of the inflorescence pubescent, often densely so, with short glandular hairs. Stem green, frequently the nodes and axes of the racemes, sometimes the entire stem, purple, soft and often conspicuously flattened in pressing and then occasionally appearing winged. Leaves pale to dark green or occasionally reddened, translucent or, less commonly, opaque; those between the middle and summit of the stem the largest, (1–)2–6.5 cm long, 0.8–4 cm wide, becoming gradually to abruptly reduced upward and ultimately bractlike and alternate, gradually to abruptly reduced downard, infrequently the leaves crowded and appearing whorled. Leaves narrowly ovate to broadly triangular, acute or very short acuminate at the apex, truncate or, more commonly, cordate at the base, sharply dentate to serrate, the teeth acutely tipped; glabrous or pubescent along the veins and occasionally also on the interveinal areas above with soft, short, falcate hairs 0.1–0.2 mm long, sometimes also with strigillose hairs, 0.1–0.3 mm long, intermixed, the undersurface glabrous or, less commonly, with short falcate hairs along the veins, the marginal cilia falcate to nearly straight, 0.1–0.3 mm long.

Petioles 0.7–2(–3) cm long, subterete to terete, commonly flattened in pressing and sometimes appearing winged, glabrous or sparsely pubescent, at least in lines above, with short, upwardly curved falcate hairs 0.1–0.2 mm long, with or without reduced branches arising in the axils. Inflorescence densely to sparsely pubescent with soft, short capitate and clavate-tipped glandular hairs 0.1–0.2 mm long, terminal on the main stem and uppermost axillary branches and occasionally at the tips of axillary branches arising at the base of the stem; green or commonly purple. The inflorescence a simple raceme or with one or two, rarely more, lateral racemes arising from the base, these subtended by reduced leaves or leaflike bracts. Flowering pedicels 0.7–1.6 mm long, glabrous or pubescent with glandular hairs as on the stem, occasionally, at maturity of the fruit, with a few uncinate hairs as on the fruit extending downward near the apex; ascending or erect, the flowers opening before elongation of the raceme and clustered at the tip; with a setaceous bracteole 0.1–0.3 mm long at the base. Fruiting pedicels 2–3.5 mm long. Buds glabrous, from the summit of the ovary, 0.9–1.6 mm long, 0.4–0.5 mm thick, white or pink, often purple tinged apically and occasionally purple throughout, ovate to broadly elliptic or obovate in outline, minutely mammiform or rounded at the apex. Ovary 0.6–1.2 mm long, 0.4–0.5 mm thick, elliptic, clavate or obovate in outline, glabrous or very rarely, with minute uncinate hairs at anthesis. Floral tube appearing as a mere constriction at the summit of the ovary to 0.4 mm long, ca. 0.2 mm thick at the narrowest point, broadly to very broadly funnelform. Sepals 0.8–1.5 mm long, 0.6–0.9 mm wide; white or pink, often tinged with purple at the apex and occasionally purple throughout, ovate to broadly ovate to oblong ovate, rounded or minutely mammiform at the apex. Petals 0.6–1.5 mm long, 0.6–1 mm wide, longer than wide, white or pink, obtriangular to obovate in outline; the apical notch absent or to 0.3 mm deep, to 1/5 the length of the petal; the petal lobes, when present, truncate to rounded. Filaments 0.7–1 mm long; anthers 0.2–0.3 mm long, 0.2–0.3 mm deep. Style 0.6–1.4 mm long; stigma 0.1–0.3 mm tall, 0.2–0.4 mm thick. Mature fruit clavate, rounded at the apex, 2.2–2.7 mm long, 0.8–1(–1.2) mm thick; the uncinate hairs 0.4–0.5 mm long, translucent and clear or occasionally containing purple pigment. Combined length of pedicel and mature fruit 4–6(–7.5) mm long. Gametic chromsome number, unknown.

TYPE: China, Gansu, at the temple of Tcheibsen-hit, 9,000 ft, 30 August 1901, *V. Ladygin 514* (LE, holotype).

Distribution (Fig. 21): Moist places, grassy alpine areas, thickets and coniferous forests at high elevations. Western China and northern Burma through the Himalayas to northwestern India. Between 3,100–5,000 m. Flowers, early June to mid-September and sporadically to mid-October.

Specimens examined:

BHUTAN. Rarder, *R. E. Cooper 784* (E); Zado La Gimpu, *R. E. Cooper 2733* (BM, E); Singhi Kivited, *R. E. Cooper 4299* (BM, E); Gafoola, upper Pho Chu, *F. Ludlow et al. 16745* (BM, E, G, UPS); Rudd La, *F. Ludlow et al. 20969* (BM).

BURMA. Maikaba-Salween divide, Mt. Chimi-li, *G. Forrest 24965* (E, NY, P, US, W).

CHINA. GANSU: Xiahe Hsien, *K. T. Fu 1048* (PE); temple of Tcheibsen-hit, *V. Ladygin 514* (LE); Xigu Hsien, *T. P. Wang 1446* (PE). SICHUAN: Pinwu Hsien, *K. L. Chu 3791* (NAS); Dege, *S. X. Jia 226* (PE); Quanning Hsien, *X. Li 5716, 5798, 5801* (PE); Dege, *X. Li 7398* (PE); Litang Hsien, *X. Li*

74248, 74337 (PE); O-pien Hsien, *S. L. Sharg 1069* (US); Dongrergo, Kuan-yin-miao, *H. Smith 3605* (S, UPS); Dara-tha-phong, *J. A. Soulie 94* (K); Take Hsien, *Take Exped. 7398* (PE); Pinwu Hsien, *H. L. Tsiang 10889* (NAS); Barkam Hsien, *C. L. Wu 32039, 32728* (PE); Ebian Hsien, *Z. W. Yao 2784, 4343* (PE); Leibo Hsien, *T. T. Yü 3811* (PE). XIZANG (TIBET): Mekong valley near Chor-chiu R., *V. Ladygin 522* (LE); Kongbo Prov., Tumbatse, Rong Chu, *F. Ludlow et al. 5106* (BM, E, UPS); Nyingchi Hsien, *Nyingchi Exped. 751269* (PE); Yadong Hsien, *Quinghai-Xizang Exped. 742476* (PE); Ka-lung-yuan ("Karlong" or "Kalungan"), *H. Smith 4113* (LD, S, UPS); Taofu dist., Haintze-shan, *H. Smith 11343* (S, UPS); Sog Hsien, *D. D. Tao 11008* (PE); Cona Hsien, *C. Y. Wu 751104* (PE); Chang'yab, *Xizang Scien. Exped. 12271* (PE); Riwage, *Xizang Scien. Exped. 12829* (PE); Bomi Hsien, *J. S. Yang & T. Y. Hong 867* (PE). YUNNAN: Fang-yang-ch'ung, *J. M. Delavay in 1887* (P); Tsa-warung, Chi-na-tang, *C. W. Wang 65343* (A, NAS, PE); War-Kar-boo, *C. W. Wang 66270* (NAS); Weixi Hsien, Yeh-chih, *C. W. Wang 68463* (A, NAS, PE); Huan-fu-ping, A-tun-tze, *C. W. Wang 68863* (NAS); Degen, *C. W. Wang 69079* (PE); Techen Hsien, Huan-fu-ping, A-tun-tze, *C. W. Wang 69725* (A, NAS, PE).

INDIA. SIKKIM: Yeumthang, Zemu & Lhonakh valleys, *G. H. Cave 173/47* (E); Lachung Valley, Yeumtang, *G. A. Gammie 782* (MIN); "Sikkim, 9–12,000 ft.," *J. D. Hooker s.n.* (BM, G, GOET, L, P, S, W); Kaljonuie, *Dr. King's collector in 1888* (W); Zemu Valley, *Smith & G. H. Cave 1680* (B). STATE UNKNOWN: Bashar, above Chasu, *J. H. Lace 400* (E).

NEPAL. Tudam, *Beer et al. 8376* (BM); Jangla Banyang, *E. Einarsson et al. 3385* (BM, L); Singalila, Sandakphu, Kalapokhari, *H. Hara et al. 69916* (TI); Singalila, Mt. Singalila, *H. Hara et al. 69917* (TI); Lari, *A. Maire 404* (BM); between Mouma & Wallun chun Gola, *K. Nishioka 1253* (KYO); Khola Kharka, *O. Polunin 1069* (BM); Thakurji Lekh, S of Jumla, *O. Polunin et al. 4754* (BM, E, UPS); near Sirtibang Lekh, *J. D. A. Stainton et al. 3453* (BM, E); Annapurna Himal., Tati Khola, *J. D. A. Stainton et al. 6676* (BM); Bhararate Himal., Barun valley, Yangle pasture, *T. Wraber 317, 334* (BM).

PAKISTAN. Chon, Thana, *without collector in 1871* (LIV).

Circaea alpina subsp. *micrantha* differs from subsp. *alpina* only in minor ways. Skvortsov (1977), in describing *C. alpina* subsp. *micrantha* as a new species, pointed out these differences, which include generally smaller floral parts, entire to barely emarginate petals with the apical notch one-fifth or less the length of the petal, glabrous ovaries at anthesis, usually densely glandular inflorescence axis, and leaves that are generally more slender and tapering and more coarsely dentate or serrate than in subsp. *alpina*. The whitened or pale undersurface of the leaves is not restricted to subsp. *micrantha* as Skvortsov suggests. Although plants referred here to *C. alpina* subsp. *micrantha* have in the past been considered the same as subsp. *alpina*, it seems best to treat the two as distinct, at least until experimental data are available.

Circaea alpina subsp. *micrantha* grows at higher elevations than any of the other subspecies of *C. alpina* and is restricted to the Himalayan region and the mountains of western and southwestern China. As delimited here, the range of *C. alpina* subsp. *micrantha* is isolated from that of subsp. *alpina* by nearly 1,000 km and overlaps aerially the ranges of subspp. *angustifolia* and *imaicola*. For the most part, it is separated from the latter two altitudinally.

INTERSPECIFIC HYBRIDS

The following are descriptions and discussions of the known hybrids in *Circaea*. Hybrids involving the bilocular species of *Circaea*, arranged in alphabetical order of the parental species, are treated first followed by hybrids involving the unilocular members of the genus.

Three hybrids (*Circaea* × *decipiens*, *C.* × *mentiens* and *C.* × *skvortsovii*), for which sufficient evidence is available to determine their parentage with cer-

tainty, are given formal names in keeping with the precedent set by the naming of *C.* × *dubia*, *C.* × *intermedia* and *C.* × *ovata*. The remaining hybrids are in need of more detailed field work to confirm the suspected parentage and are here listed under the hybrid combination of the probable parents.

Circaea × *dubia* Hara (*Circaea cordata* Royle × *Circaea erubescens* Franchat & Savat.), Bot. Mag. Tokyo 50: 306. 1936.—FIG. 27.

Morphologically intermediate between *Circaea cordata* and *C. erubescens*. Erect, rarely decumbent at the base, 2–10(–15) dm tall, simple or freely branched above, forming vigorous, long, often branched, rhizomes which give rise to the following year's plants from their tips. Plants sparsely to densely pubescent; the stem with soft, short, falcately recurved hairs, 0.2–0.4 mm long; the inflorescence with short, capitate and clavate-tipped, glandular hairs or short falcately recurved hairs as on the stem, or these intermixed, also with a few long, straight or slightly curved, sharp pointed, soft hairs, 0.4–1 mm long; the petioles with upwardly curved falcate hairs as on the stem; the leaves with pubescence as on the petioles and also with scattered, long, straight hairs, 0.7–1.2 mm long. Stem green, the nodes purple. Leaves horizontally spreading, usually drooping at the tips, green, opaque; those slightly above the middle of the stem the largest, 5.5–15 cm long, 3.5–8.5 cm wide; becoming gradually reduced in size upward to the inflorescence and eventually bractlike and alternate, gradually reduced in size downward (although not always apparent since the lower leaves are usually deciduous by flowering time); narrowly to broadly ovate, short to long acuminate at the apex, rounded to subcordate at the base, denticulate; densely pubescent, at least above; the veins with falcate hairs, 0.2–0.4 mm long, and with long, slightly curved or straight hairs, 0.7–1.2 mm long; the interveinal areas with short, falcate hairs, 0.2–0.3 mm long, and/or with erect or strigillose hairs, 0.2–0.4 mm long; the margins with dense falcate cilia, 0.1–0.2 mm long, and/or with straight or slightly curved hairs, 0.2–0.4 mm long. Petioles 3–6(–7.5) cm long, densely pubescent with upwardly curved, falcate hairs, 0.2–0.4 mm long and with longer, straight or slightly curved hairs, 0.3–0.5 mm long, sometimes also with long, straight, sharp pointed, soft hairs, 0.7–1.1 mm long, intermixed; often with reduced branches arising in the axils. Inflorescence sparsely to densely pubescent with short, capitate and clavate tipped, glandular hairs, 0.1–0.2 mm long, or with falcately recurved hairs, 0.2–0.5 mm long, or with an admixture of the two, occasionally also with long, straight or slightly curved, patent hairs, 0.7–1.2 mm long, intermixed; terminal on the main stem and often at the tips of the uppermost axillary branches; the racemes simple or branched at the base, the lower branches alternate or opposite and subtended by reduced leaves or leaflike bracts. The terminal raceme, from the uppermost reduced leaf or leaflike bract, 1–2 cm long at initiation of flowering, to 12(–18) cm long at cessation of flowering; the lateral racemes ca. 2–3 cm long at initiation of flowering, to 8(–15) cm long at cessation of flowering, subequal to variable in length on the same plant. Flowering pedicels 1.1–2.8 mm long, perpendicular to the axis of the raceme, glabrous or pubescent, with short capitate and clavate-tipped, glandular hairs, 0.1–0.2 mm long, and occasionally with long, straight hairs, 0.4–1 mm long, with a setaceous bracteole, 0.1–0.7 mm long, at the base; closely spaced, the flowers clustered near the apex

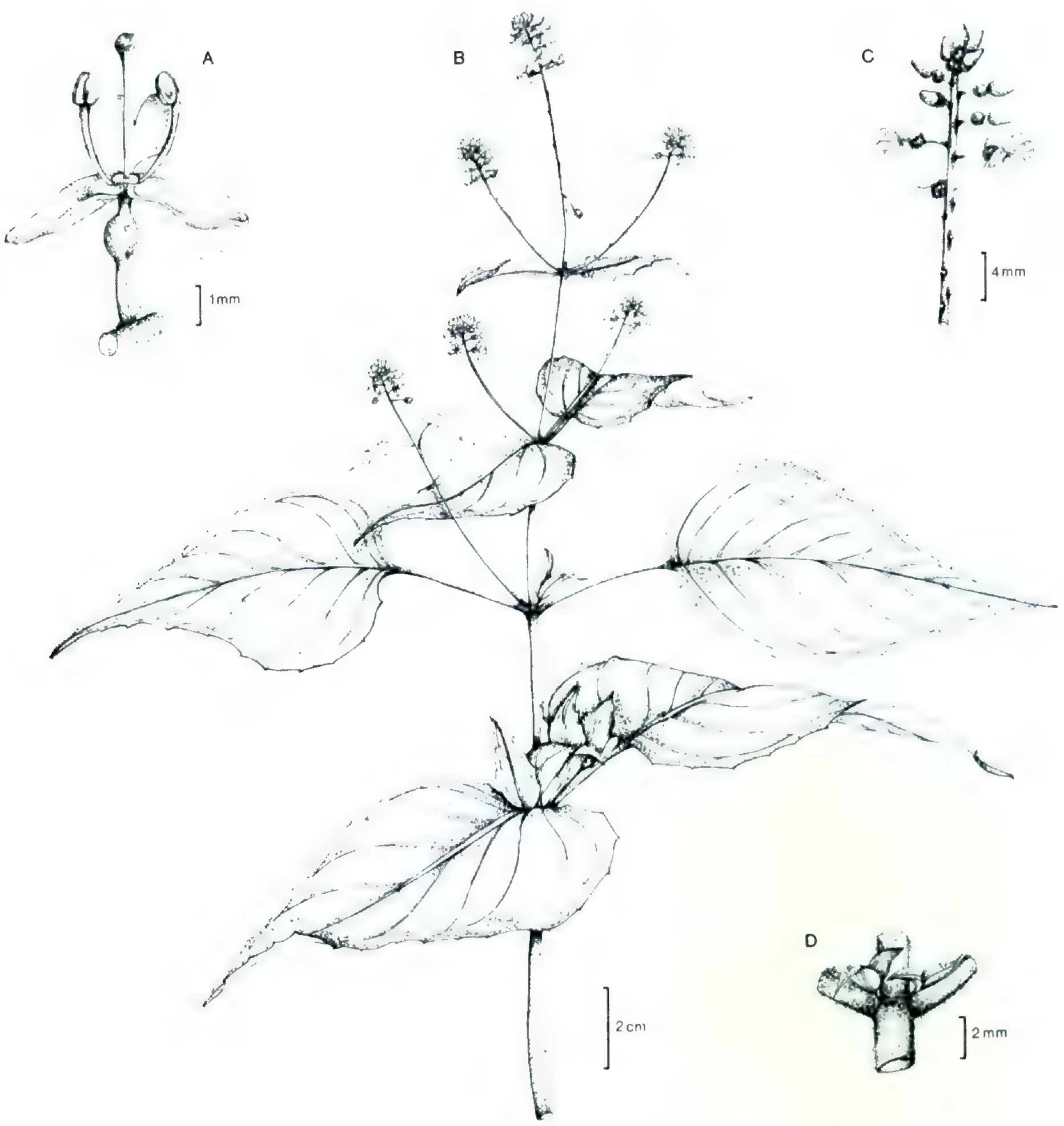


FIGURE 27. *Circaea* × *dubia* Hara (*C. cordata* Royle × *C. erubescens* Franchet & Savat.).—A. Flower with petal removed; note low, exserted nectary.—B. Upper flowering stem.—C. Inflorescence. Upper node of stem. From *Boufford et al. 19578* (MO).

of the raceme. Fruiting pedicels developing to 2.7 mm long before abortion of the fruits. Buds glabrescent to pubescent, with short, glandular hairs ca. 0.1 mm long and/or with long, sharp pointed, straight or abruptly bent hairs, 0.5–0.9 mm long; white, pink or very pale green; narrowly to broadly elliptic or oblong in outline, rounded gradually or acuminate to the obtuse or minutely mammiform apex; from the summit of the ovary, 2.6–3.6 mm long just prior to anthesis. Ovary 1.1–1.8 mm long, 0.6–1.9 mm thick at anthesis, very thickly lenticular to pyriform, very densely covered with soft, translucent, uncinate hairs. Floral tube 0.6–0.9 mm long, 0.1–0.2 mm thick at the narrowest point, funnelform or the sides tapering concavely to the ovary, glabrous or pubescent, with short glandular hairs and/or with long straight hairs as on the buds. Sepals 1.9–2.9 mm long, 0.8–1.9 mm wide, glabrous or pubescent on the abaxial surface with hairs as on the buds;

white or pink; lanceolate oblong to very broadly elliptic or broadly oblong, gradually rounded to long acuminate to the minutely mammiform or obtuse apex, divergent to reflexed in flower. Petals 1.3–2.2 mm long, 1.2–2.2 mm wide, more commonly wider than long, white or pink, obovate, obdeltoid to transverse obovate in outline; the apical notch 0.4–0.9 mm deep, ⅓–½, rarely more, the length of the petal, the petal lobes rounded to minutely crenulate. Stamens spreading at anthesis, shorter than or occasionally equalling the style; filaments 1.2–2.7 mm long; anthers 0.5–0.7 mm long, 0.3–0.5 mm thick. Style erect, straight or slightly drooping at the tip, 3.4–4.3 mm long, topped by an obconic to transverse, narrowly oblong, prominently bilobed stigma, 0.3–0.5 mm tall, 0.4–0.7 mm thick. Nectar secreting disc present as a low exserted ring at the summit of the floral tube, ca. 0.1 mm tall, 0.3–0.6 mm thick, more obvious in living plants. Mature fruit very rarely developing, when present, 2.2–3.2 mm long, 1.5–2.5 mm thick, thickly lenticular to flattened pyriform to obovoid, often with one or both seeds failing to develop to maturity; bilocular, without prominent ribs or sulci, densely covered with stiff, translucent, uncinate hairs, 0.8–1.1 mm long, and with shorter, capitate and clavate-tipped, glandular hairs. Fruiting pedicels, when present, slightly reflexed. Gametic chromosome number, $n = 11$ (9 bivalents plus a ring or chain of 4 at meiosis).

TYPE: Japan, Hokkaido, Hidaka-shicho, in forests near Shoya, 11 August 1934, *H. Hara C4689* (TI, holotype).

Distribution: Sporadic but often abundant in naturally, rarely man-caused, disturbed areas; commonly along streams, in broad-leaved temperate deciduous forests. Hokkaido, and Honshu, Japan; northeastern China. From near sea level to ca. 1,500 m. Flowers, mid-July to late August, rarely into September.

Representative specimens examined:

CHINA: Manchuria, 1941, *no further data* (MAK). JAPAN. HOKKAIDO: Abashiri-shicho, along the Okoppe-gawa River at the Sako-hashi bridge, *D. E. Boufford & E. W. Wood 19798* (BM, CAS, CM, E, G, K, KYO, MHA, MO, P, SHIN). Abashiri-shicho, Okoppe-cho, 15.9 km NE of Nishiokoppe on hwy 239, *D. E. Boufford & E. W. Wood 19806* (KYO, MHA, MO). Hidaka-schicho, forests near Shoya, *H. Hara C4689* (TI). Hidaka-shicho, Samani-gun, Samani-cho, Okada, *D. E. Boufford & E. W. Wood 19697* (BM, C, CAN, CAS, CM, E, G, GH, K, KYO, LD, LE, MA MHA, MICH, MO, NCU, NY, P, PE, S, SHIN, TUS, UC). Ishikari-shicho, Sapporo city, Mt. Teine-yama, *H. Yanagirawa in 1915* (SAPS). Kawakami-shicho, hwy 40 just WNW of Osashima at border of Nakagawa-cho, *D. E. Boufford & E. W. Wood 19830* (KYO, MO). HONSHU: FUKUSHIMA PREFECTURE, Nishigo-mura, Iwaki, *S. Suzuki* (TNS 42101), Nishi-shirakawa-gun, Saigo-mura, Saigo-cho, *T. Suzuki in 1933* (KYO). HYOGO PREFECTURE, Yabu-gun, Sekinomiya-cho, en route from Fukusada to the summit of Mt. Hyonosen, *G. Murata 21100* (KYO), (Tajima Province), Mt. Hyonosen, *S. Kitamura & G. Murata 634* (KYO), Mikata-gun, Onsen-cho, Kiri-taki waterfall, *G. Murata 20683* (KYO), *D. E. Boufford, E. W. Wood & K. Iwatsuki 19595* (BM, CM, E, G, GH, K, KYO, LD, MHA, NCU, P, PE, S, SHIN, TI, TUS, UC), Yabu-gun, Oya-cho, Ikada, Ten-taki waterfall, *G. Murata 22071* (KYO), *D. E. Boufford, E. W. Wood & K. Iwatsuki 19584* (CM, KYO, MO), Shiso-gun, Haga-cho, Tokura, *G. Murata 20364* (KYO, MAK, TI, TNS), *D. E. Boufford, E. W. Wood & K. Iwatsuki 19587* (BM, CM, G, K, KYO, MHA, MO, NCU, PE, SHIN, TUS). IWATE PREFECTURE, Kawanuma-gun, Kanagami-mura, Iwashiro, *in 1893* (TNS 32183). NAGANO PREFECTURE, Chino city, Oyayu, *in 1925* (MAK 117793), Shinano, Mt. Kirigamine, *H. Takei* (TNS 117073), Shinano, Mt. Tateshima, *H. Takei* (TNS 106456), Kita-saku-gun, Asama, *M. Goto* (MAK 117769), Minami-saku-gun, Mt. Goza, Yamaguchi-michi, *H. Hara in 1958* (TI), Nichino, Kaida village, Kiso, *M. Mizushima in 1953* (TI), Shiraiwa-dake, Miwa-mura, *S. Korayama in 1958* (TI), Kamiina-gun, Miwa-mura, Todai, *G. Murata 7999* (KYO, SAPS). NIGATA PREFECTURE, Minami-uonuma-gun, Mimata-mura, Yagi-sawa, *K. Teramoto in 1946* (TI). SHIZUOKA PREFECTURE, Mt. Fuji-san, Maotenjin, *B. Hayata in 1924* (TI). TOCHIGI

PREFECTURE, Nasu, (cultivated) *H. Hara in 1957* (TI). TOKUSHIMA PREFECTURE, Miyoshi-gun, Mikamo-machi, Sajiki-toge pass, *M. Takafuji 864* (KYO). TOTTORI PREFECTURE, Iwami-gun, Hokubu-cho, Mt. Ojinosen, *A. Tanaka 20556* (KYO). YAMANASHI PREFECTURE, Yamanaka-ko Lake, foot of Mt. Fuji-san, *B. Hayata in 1929* (TI). SHIKOKU: KOCHI PREFECTURE (Tosa Province), Nanogawa-mura, *K. Watanabe* (TNS 53627), Tosa-gun, Tosayama-mura, Mt. Kuichi, *T. Yamanaka 43169, 46786* (TNS), *T. Makino in 1887* (MAK 6950). Toyobishi, no further data, *S. Hori* (MAK 117750).

Circaea × *dubia* (*C. cordata* × *C. erubescens*) is by far the most common hybrid of *Circaea* in Japan and perhaps in all of eastern Asia. Its occurrence in Japan parallels the situation in North America and Europe where hybrids between *C. alpina* and *C. lutetiana* are often found in the absence of one or both parental species. *Circaea* × *dubia* is most common along, but not restricted to, stream margins where frequent flood waters often remove less agressive plants. *Circaea* × *dubia* occurs commonly in the zone between the lowest waters of the summer and the highest spring floods and may extend along streams for several kilometers, as along the Okkoppe-gawa River in north-central Hokkaido. Other habitats in which *C.* × *dubia* may be found are in alluvial woods in low depressions that have been scoured clean of other vegetation by flooding and in seepages in man-made or natural clearings. *Circaea* × *dubia* is intermediate in habitat preference between *C. cordata* and *C. erubescens*.

Hara (1936, 1959) has pointed out the morphological intermediacy of *Circaea* × *dubia* between *C. cordata* and *C. erubescens*. Despite its intermediate nature, *C.* × *dubia* is highly variable from population to population and is especially variable in degrees of pubescence. The buds especially may vary from glabrescent to densely pubescent. All plants of *C.* × *dubia* have at least a few of the long, soft hairs of *C. cordata* mixed in with shorter falcate hairs on the stem, leaves or inflorescence axes. *Circaea* × *dubia* also resembles *C. cordata* in its often robust habit, general leaf shape, and in the relatively close spacing the flowers at anthesis. The petals, also, are similar to those of *C. cordata* in shape although in color they are often pink as in *C. erubescens*. *Circaea* × *dubia* resembles *C. erubescens* in having an exserted, but often very low and inconspicuous, ringlike, nectar-secreting disc, and in having the nodes purple. Degree of pubescence is highly variable on the inflorescence axes and on the pedicels. In some plants the inflorescence is nearly glabrous while in others it is densely pubescent. Similarly, the stem also varies in degrees of pubescence, but never to the extent of the inflorescence. The sepals resemble more often those of *C. cordata*, which are broadly to very broadly elliptic or oblong, than those of *C. erubescens*, which tend to be lanceolate and short to long tapering or acuminate at the apex. The ovaries are more commonly like those in *C. cordata* in being thickly lenticular and very densely uncinate pubescent, yet the ovaries that develop closest to maturity are most often obovate and similar in shape to those of *C. erubescens*.

Pollen fertility in *Circaea* × *dubia* averaged ca. 9% fertile, ranging from 1.6 to 17.5%, with mostly normal, 3-pored grains, in 16,506 grains examined.

Circaea × *skvortsovii* Boufford, hybrid nov., = *Circaea cordata* Royle × *Circaea lutetinana* L. subsp. *quadrisulcata* (Maxim.) Asch. & Magnus.—FIG. 28.

Circaea cordatae Royle simile, in nectario exsertio differt, et C. lutetiana L. subsp. quadrisulcatae (Maxim.) Asch. & Magnus. simile, sed in caule pubenti differt.

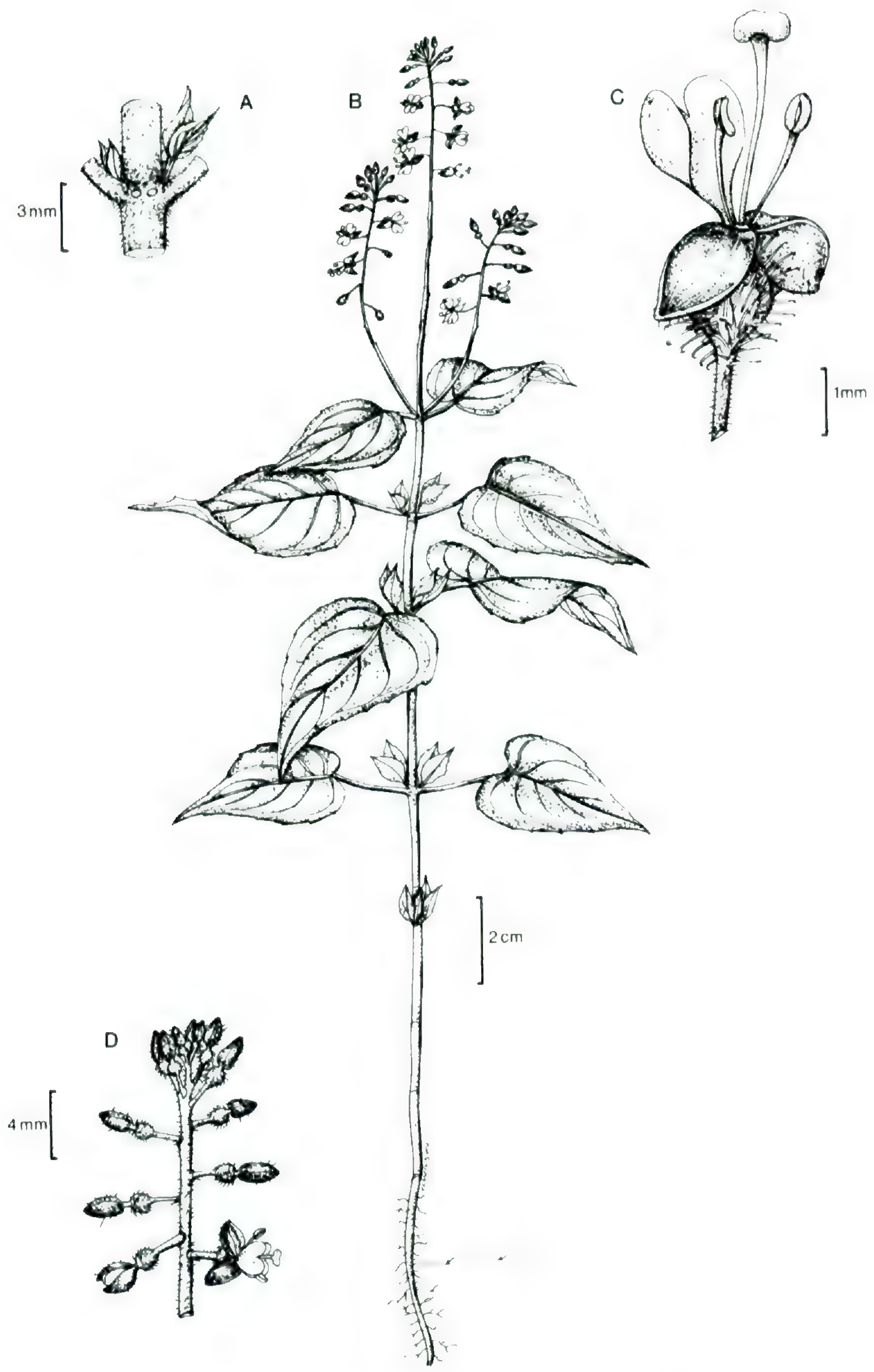


FIGURE 28. *Circaea* × *skvortsovii* Boufford (*C. cordata* Royle × *C. lutetiana* L. subsp. *quadrisulcata* (Maxim.) Asch. & Magnus.—A. Mid-stem node.—B. Habit.—C. Flower with petal removed; note low, exserted nectary.—D. Inflorescence. From *Alexeeva in 1973* (MHA).

Morphologically intermediate between *Circaea cordata* and *C. lutetiana* subsp. *quadrisulcata*. Erect, 2.2–6 dm tall, simple below the inflorescence, forming long, non-tuberous rhizomes which give rise to the following year's plants from their tips. Plants sparsely to densely pubescent; the stem with soft, short, falcately recurved hairs ca. 0.2 mm long and with occasional long, straight or slightly

curved, patent hairs to ca. 0.8 mm long; the inflorescence with soft, short, capitate and clavate-tipped, glandular hairs, 0.2–0.3 mm long and with a few, long, straight or slightly curved, patent hairs, 0.4–0.8 mm long intermixed; the petioles with upwardly curved falcate hairs, 0.2–0.4 mm long, these continuing along both surfaces of the leaf, the leaf also with short, straight, soft hairs ca. 0.2 mm long, these appearing strigillose in pressed specimens. Stem green. Leaves horizontally spreading, flat or drooping at the tips, green or slightly grayish, opaque; those slightly above the middle of the stem the largest, 4.5–6.5 cm long, 2.5–3.5 cm wide; becoming gradually reduced in size upward and eventually bractlike and alternate in the lower part of the inflorescence, gradually reduced in size downward (although not always apparent since the lower leaves are usually deciduous by flowering time); narrowly to broadly ovate to oblong ovate, short-acuminate at the apex, truncate to subcordate or cordate at the base, denticulate, sparsely to densely pubescent; the leaf margins with straight and falcate cilia, 0.2–0.4 mm long. Petioles 1.2–4 cm long, densely pubescent with upwardly curved, falcate hairs, 0.2–0.4 mm long; with reduced branches arising in the axils. Inflorescence densely pubescent with glandular hairs, 0.2–0.3 mm long, and with long, straight or slightly curved, patent hairs, 0.4–0.8 mm long; terminal on the main stem and less frequently (?) at the tips of the uppermost axillary branches, the racemes simple or, more commonly, branched at the base, when branched, the branches commonly alternate, subtended by reduced leaves or leaflike bracts; the terminal raceme, from the uppermost reduced leaf or leaf-like bract, ca. 1.5 cm long at initiation of flowering, to ca. 10 cm long at cessation of flowering; the lateral racemes ca. 2 cm long at initiation of flowering, to ca. 6 cm long at cessation of flowering, subequal in length on the same plant. Flowering pedicels 1.8–3 mm long, perpendicular to the axis of the raceme, pubescent with short, capitate and clavate-tipped, glandular hairs, 0.2–0.3 mm long, and with a few straight or slightly curved, sharp pointed hairs to ca. 0.5 mm long; ± closely spaced, the flowers clustered near the apex of the raceme; with a setaceous, sometimes caducous bracteole, 0.2–0.4 mm long, at the base. Fruiting pedicels apparently failing to develop. Buds pubescent with short, glandular hairs, 0.1–0.2 mm long; purple, except for the floral tube, broadly elliptic oblong to oblong in outline, rounded to the obtuse or minutely mammiform apex, from the summit of the ovary, 2.4–3.2 mm long, 1.2–1.3 mm thick just prior to anthesis. Ovary 1.1–1.7 mm long, 1–1.5 mm thick at anthesis, thickly lenticular to flattened obovate, very densely covered with soft, short, translucent, uncinate hairs. Floral tube 0.4–0.5 mm long, 0.2–0.3 mm thick at the narrowest point, subcylindric to broadly funnelform, pubescent, with glandular hairs, 0.1–0.2 mm long. Sepals 2.2–2.8 mm long, 1.4–1.6 mm wide, pubescent on the abaxial surface with hairs as on the buds; pink or purple. Broadly elliptic oblong to oblong ovate, rounded to the obtuse or minutely mammiform apex, divergent to reflexed in flower. Petals 1.6–2.4 mm long, 2–2.4 mm wide, commonly wider than long, pink or white, depressed broadly obovate in outline; the apical notch 1–1.3 mm deep, from slightly less to slightly more than ½ the length of the petal; the petal lobes broadly rounded. Stamens spreading at anthesis, shorter than to nearly equalling the style; filaments 1.5–2 mm long; anthers 0.4–0.5 mm long, ca. 0.4 mm thick. Style straight, erect, ca. 3.2 mm long, topped by an obconic to transversely oblong, often prominently

bilobed stigma, 0.4–0.5 mm tall, 0.6–1 mm thick. Nectar-secreting disc present as a low ring at the summit of the floral tube, ca. 0.1 mm tall, 0.3–0.5 mm thick, more obvious in living material. Mature fruit not seen. Ovary bilocular and 2-seeded, the seeds evidently not fertile. Gametic chromosome number, unknown.

TYPE: U.S.S.R., Sakhalin, Moneron Island (Kaibato), 16 August 1973, *L. Alexeeva s.n.* (MHA, holotype).

Distribution: Disturbed habitats. Northeastern China, Far Eastern U.S.S.R. and northern Japan. Flowers, August.

Representative specimens examined:

CHINA. HEBEI: Hsiang-shan region, *H. Sheehan 462* (NY). Chili, Trappist Monastery, *J. Liu 1024* (UC). "MANCHURIA," Korean Gate ("Korii-mon") *Kitagawa in 1931* (TI). JAPAN. HONSHU: IWATE PREFECTURE: Shimohei-gun, Mt. Hachine, *T. Makino in 1905* (MAK 6953). U.S.S.R.: Sakhalin, Moneron Island (Kaibato), *Alexeeva in 1973* (MHA), *E. Egorova 2533* (MHA).

Circaea × *skvortsovii* (*Circaea cordata* × *C. lutetiana* subsp. *quadrisulcata*) is most obviously intermediate between the two parents in degree and nature of the pubescence and in the morphology of the floral parts. It is similar to *C. cordata* in having long, sharp pointed, straight or slightly curved patent hairs occurring sporadically on various parts of the plant and in having the stem pubescent. In color of the buds, sepals, and petals, in the presence of a low, exserted nectary projecting beyond the opening of the floral tube, and in the dense glandular pubescence of the inflorescence axis, it is similar to *C. lutetiana* subsp. *quadrisulcata,* but in shape of petals and relatively close spacing of the flowers it is more like *C. cordata*. The presence of a setaceous bracteole at the base of the pedicels in this hybrid is also characteristic of *C. cordata*.

Circaea × *ovata* (Honda) Boufford stat. nov. (*Circaea cordata* Royle × *Circaea mollis* Siebold & Zucc.). Based on *C. quadrisulcata* (Maxim.) Franchet & Savat. var. *ovata* Honda, Bot. Mag. Tokyo 46: 3. 1932.—FIG. 29.

Circaea mollis Siebold & Zucc. var. *ovata* (Honda) Hara, J. Jap. Bot. 10: 598. 1934.

Morphologically intermediate between *Circaea cordata* and *C. mollis*. Erect, 3–1.3 dm tall, simple or freely-branched above, forming long, often branched, non-tuberous rhizomes which give rise to the following year's plants from their tips. Plants densely pubescent; the stem grayish or whitish green with short and long falcately recurved hairs, 0.2–0.4 mm long; the inflorescence with hairs as on the stem and occasionally with long, straight or slightly curved, sharp pointed, soft hairs, 0.4–1.1 mm long and sometimes also with short, capitate and clavate tipped, glandular hairs, 0.1–0.2 mm long; the petioles with upwardly curved falcate hairs as on the stem and often also with long, straight or slightly curved hairs, 0.4–1.1 mm long, the falcate hairs continuing along the main veins of the leaf, at least above, the interveinal areas with erect straight hairs, 0.2–0.4 mm long, these appearing strigillose in pressed specimens, and often also with short falcate hairs intermixed. Stem green or grayish, the nodes purple. Leaves horizontally spreading, drooping at the tips, green or grayish, opaque; those slightly

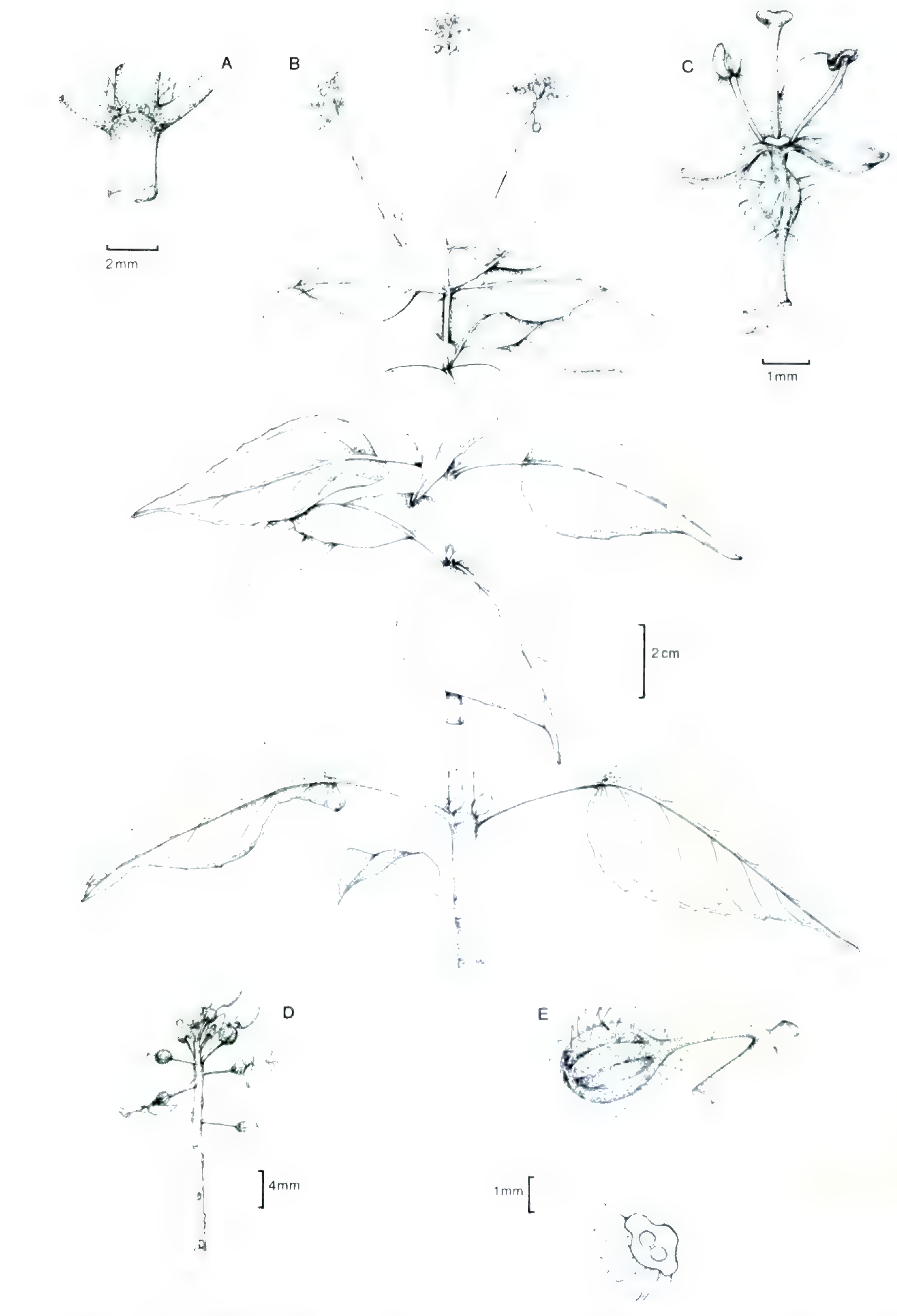


FIGURE 29. *Circaea* × *ovata* (Honda) Boufford (*C. cordata* Royle × *C. mollis* Siebold & Zucc.).—A. Mid-stem node.—B. Mid and upper flowering stem.—C. Flower with petal removed; note low, exserted nectary.—D. Inflorescence.—E. Developing fruit. From *Boufford & Wood 19855* (K, KYO, MHA, MO, S, SHIN).

above the middle of the stem the largest, 7–12 cm long, 4–6.5 cm wide; becoming very gradually reduced in size upward and eventually bractlike and alternate in the lower part of the inflorescence, gradually reduced in size downward (although not always apparent since the lowest leaves are usually deciduous by flowering time); ovate lanceolate to ovate, short to long acuminate at the apex, rounded or, less commonly, subcordate at the base, denticulate, sometimes very minutely so; densely pubescent, with hairs as on the petiole continuing along the veins and also often on the interveinal areas, at least above, the interveinal areas also with erect, straight hairs, 0.2–0.4 mm long, these often appearing strigillose in pressed specimens; the leaf margins with short falcate cilia, ca. 0.2 mm long, and with longer, straight or slightly curved hairs, 0.2–0.4 mm long. Petioles 1.5–6 cm long, densely pubescent with upwardly curved, falcate hairs, 0.1–0.4 mm long, and often with longer, straight or slightly curved hairs, 0.4–0.9 mm long intermixed; with reduced branches arising in the axils. Inflorescence densely pubescent with short, falcately recurved hairs, 0.1–0.2 mm long and longer, slightly recurved hairs, 0.2–0.4 mm long, often with long, straight, sharp pointed hairs, 0.4–1 mm long intermixed, less commonly also with short, glandular hairs, 0.1–0.2 mm long; terminal on the main stem and often at the tips of the uppermost axillary branches or directly from the uppermost leaf axils, the racemes simple or branched at the base, when branched, the branches commonly opposite or subopposite, subtended by reduced leaves or leaflike bracts; the terminal raceme, from the uppermost reduced leaf or leaflike bract, ca. 2 cm long at initiation of flowering, to ca. 12 cm long at cessation of flowering; the lateral racemes 1.5–3 cm long at initiation of flowering, to ca. 9 cm long at cessation of flowering, subequal in length on the same plant. Flowering pedicels 1.1–2.8 mm long, perpendicular to the axis of the raceme, pubescent with short, glandular hairs, 0.1–0.2 mm long, and often with short, falcately recurved hairs, 0.1–0.2 mm long; closely spaced, the flowers clustered near the apex of the raceme; with a setaceous, sometimes caducous, bracteole, 0.3–0.6 mm long, at the base. Fruiting pedicels developing to ca. 2.7 mm long before abortion of the fruits. Buds pubescent with short glandular hairs, 0.1–0.2 mm long, and occasionally also with long, straight or slightly curved hairs, to ca. 0.5 mm long; white or pale green, very broadly elliptic to subcircular in outline, rounded to the obtuse tip; from the summit of the ovary, 2.6–2.8 mm long, 1.1–1.4 mm thick just prior to anthesis. Ovary 1.2–2.1 mm long, 0.9–1.8 mm thick at anthesis, thickly lenticular to flattened obovoid, very densely covered with soft, translucent, uncinate hairs. Floral tube 0.5–0.7 mm long, 0.1–0.35 mm thick at the narrowest point, funnelform, pubescent with short glandular hairs, 0.1–0.2 mm long. Sepals 1.9–3.2 mm long, 1.1–1.9 mm wide, pubescent on the abaxial surface with hairs as on the buds, white or very pale green, oblong to very broadly elliptic, rounded to the obtuse apex, divergent to reflexed in flower. Petals 1.8–2.4 mm long, 1.9–2.6 mm wide, wider than long, white, broadly obovate to depressed obovate in outline; the apical notch 0.6–1.1 mm deep, ⅓–½ the length of the petal; the petal lobes rounded, often broadly so. Stamens spreading at anthesis, shorter than, to equalling the style; filaments 2–3 mm long; anthers ca. 0.6 mm long, ca. 0.5 mm thick. Style straight, erect, 2.9–4 mm long, topped by an obconic to very narrow, transversely oblong, bilobed stigma, 0.2–0.4 mm tall, 0.6–1.4 mm thick. Nectar se-

creting disc present as a low ring at the summit of the floral tube, ca. 0.1 mm tall, 0.5–0.6 mm thick, more obvious in living material. Mature fruit very rarely developing, when present, 3.3–3.5 mm long, 2.4–2.5 mm thick, thickly lenticular to flattened, broadly obovoid, with low ribs and very shallow sulci; appearing intermediate between fruits of *Circaea cordata* and *C. mollis*; bilocular and 2-seeded, one or both seeds commonly failing to develop; densely covered with stiff, translucent, uncinate hairs ca. 0.9 mm long and with shorter, glandular hairs ca. 0.1 mm long. Fruiting pedicels, when present, sharply reflexed. Combined length of pedicel and mature fruit developing to ca. 6.5 mm long. Gametic chromosome number, $n = 11$ (9 bivalents plus a ring or chain of 4 at meiosis).

TYPE: Japan, Honshu, Tochigi Prefecture, Kamitsuga-gun, Higashioashi-mura, Mt. Futamata, 1931, *H. Sekimoto 13* (TI, holotype).

Distribution: Local in natural and man-made disturbed areas in temperate deciduous forests and *Cryptomeria* plantations. Japan, Hokkaido, and central and northern Honshu and the southern Kurile Islands (Kunashiri, one collection); China. From ca. 50 to 1,500 m. Flowers, late July to early September.

Representative specimens examined:

CHINA. SICHUAN: Nan-ch'uan, Chin-fo-shan, Chu-lung-chiao, *K. F. Li in 1957* (PE 537839). Yunnan-sen, *J. Cavalerie 212* (E). JAPAN. HOKKAIDO: Ishikari-shicho, Sapporo city, Mt. Maruyama, *M. Hara in 1942* (TI), *D. E. Boufford & E. W. Wood 19855* (K, KYO, MHA, MO, S, SHIN). Ishikari-shicho, Otaru city, I-jima, *S. Mimoro in 1975* (KYO). Ishikari-shicho, Sapporo city, Mt. Teine-yama, *Y. Takahashi in 1917* (SAPS). Shiribeshi-shicho, Yoichi, *T. Yamamoto 4428* (KYO). HONSHU: GUNMA PREFECTURE, Ose, Nebasawa, *J. Ohwi & M. Tagawa 706* (KYO). IWATE PREFECTURE, Morioka city, *G. Toba 638* (TI). KANAGAWA PREFECTURE, Yokosuka, *L. Savatier 412* (P, S). NAGANO PREFECTURE, Kiso, Mt. Ontake-san, *G. Koizumi in 1910* (TI). NIIGATA PREFECTURE, Kiyotsu-kyo, Nakauonuma-gun, *S. Kobayashi 12862* (KYO, S). SHIGA PREFECTURE, Mt. Ibuki-yama, *J. Nakai in 1910* (MAK). TOKYO PREFECTURE, Mt. Dokan-yama, *T. Makino in 1888* (MAK 6951), (Musashi Province), Nishi-tama-gun, Mt. Kariyose, *T. Makino in 1930* (S). YAMAGATA PREFECTURE, Higashine city, *D. E. Boufford & E. W. Wood 19881* (K, KYO, MO, NY, P, UC). KURILE ARCHIPELAGO. Kunashiri Island, *L. Alexeeva 5423* (MHA). SOUTH KOREA. Keisyonan-do, Mt. Chii-san, *K. Uno* 23114a (GH).

Circaea × *ovata* is totally intermediate between *C. cordata* and *C. mollis*. Next to *C.* × *dubia* (*C. cordata* × *C. erubescens*), this is the most common hybrid of *Circaea* in eastern Asia. Unlike the situation in *C.* × *dubia* where either or both parents may be absent in the presence of the hybrid, *C.* × *ovata* appears to occur only in areas where the two parents are found together, and then only if a suitable disturbed habitat is available. A single exception may be the collection of Alexeeva (MHA) from Kunashiri Island in the Kurile Archipelago, which appears to be this hybrid. *Circaea mollis* has yet to be collected in the Kuriles but *C. cordata* is present there. Unfortunately, most label data on *C.* × *ovata* fail to indicate whether or not other species are growing nearby. It will be necessary for those in a position to do so to carry on additional field work in order to determine how widespread this hybrid is and whether or not it definitely occurs in the absence of the parents.

Individual plants in a population of *Circaea* × *ovata* are remarkably similar morphologically although different populations may be quite variable, as is the case in all hybrids of *Circaea*, suggesting that hybrids are formed relatively infrequently and spread primarily by vegetative means when they are formed.

Circaea × *ovata* differs from *C. cordata* in having the nodes darkened, in the presence of a low, ringlike disc projecting above the floral tube and in having pubescence consisting of mostly curved rather than straight hairs. From *C. mollis*, *C.* × *ovata* differs in having longer recurved hairs as well as a few straight, sharp pointed hairs on at least some part of the plant, in having the nectar-secreting disc greatly reduced in height and in having the coloration of the nodes reduced in intensity. In shape of petals, ovaries (and fruits when they develop), and leaves, *C.* × *ovata* is intermediate between the two parents.

Circaea × *ovata* resembles hybrids between *C. cordata* and *C. lutetiana* subsp. *quadrisulcata* but the latter generally has the inflorescence more densely glandular-pubescent, the leaves oblong-ovate and more often subcordate to cordate at the base and buds that are often purple or pink. *C.* × *ovata* has a more southerly distribution than *C. cordata* × *C. lutetiana* subsp. *quadrisulcata* but there is some overlap of ranges in Hokkaido.

Pollen fertility in *C.* × *ovata* averages 4.2% and ranges from 0.85% to 24% in the specimens examined.

Circaea × *decipiens* Boufford, hybrid nov. = *Circaea erubescens* Franchet & Savat. × *Circaea lutetiana* L. subsp. *quadrisulcata* (Maxim.) Asch. & Magnus.—FIG. 30.

Circaea erubescentis Franchet & Savat. simile, in petalis profundioribus incisis, lobis rotundatis differt, et C. lutetiana L. subsp. quadrisulcatae (Maxim.) Asch. & Magnus simile, in inflorescentia pubescentia sparsiore differt.

Resembling *Circaea* × *dubia* (*C. cordata* × *C. erubescens*) but glabrous; intermediate between *Circaea erubescens* and *C. lutetiana* subsp. *quadrisulcata*. Erect or decumbent at the base and rooting at the nodes, 4–9.5 dm tall, simple below the inflorescence, forming non-tuberous rhizomes which give rise to the following year's plants from their tips. Plants almost totally glabrous; the stem glabrous or with a few, short, falcately recurved hairs ca. 0.2 mm long; the petioles with similar but upwardly curved, sparse hairs; the inflorescence axes with short, capitate and clavate-tipped glandular hairs 0.1–0.2 mm long, these sometimes very sparse. Stem green, the nodes purple. Leaves horizontally spreading, drooping at the tips, green, opaque; those between the middle and upper part of the stem the largest, 7–10.5 cm long, 4.5–6.5 cm wide; becoming gradually reduced in size upward to the inflorescence and eventually bractlike and remaining opposite, less commonly alternate; gradually reduced in size downward (but not always apparent since the lower leaves are usually deciduous by flowering time); oblong lanceolate to ovate to broadly so to oblong ovate, acuminate at the apex, very broadly cuneate to rounded or truncate at the base, denticulate, very sparsely pubescent above with short, falcate hairs ca. 0.2 mm long; the margins with slightly curved or falcate cilia, 0.2–0.4 mm long. Petioles 3–5 cm long, sparsely pubescent with upwardly curved, falcate or slightly curved cilia, 0.2–0.4 mm long; most often without reduced branches arising in the axils. Inflorescence essentially glabrous to densely pubescent, often varying from one raceme to another on the same plant, with short, capitate and clavate-tipped, glandular hairs; terminal on the main stem and often from the axils of the uppermost leaves; the racemes simple or the terminal raceme with lateral branches

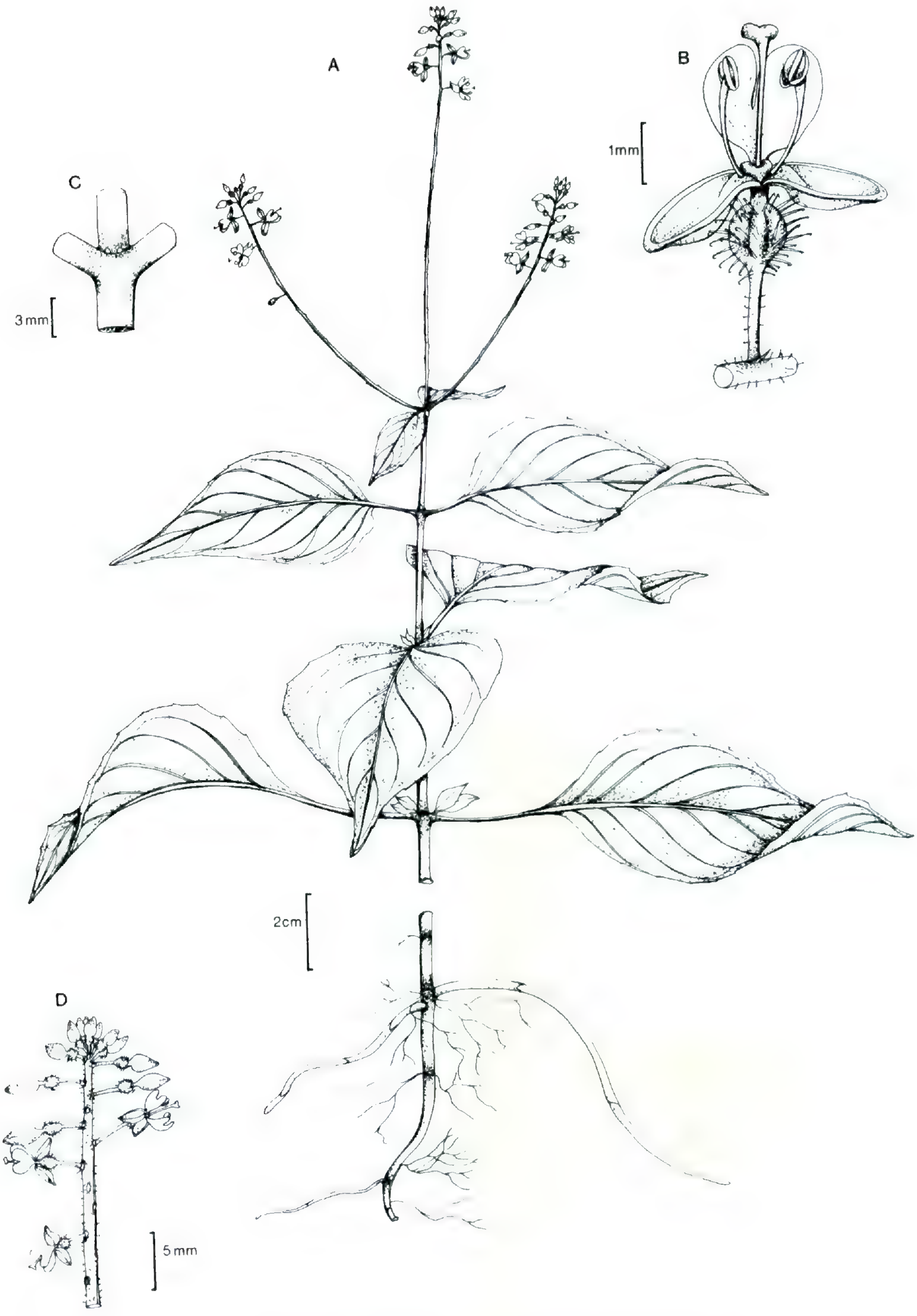


FIGURE 30. *Circaea* × *decipiens* Boufford (*C. erubescens* Franchet & Savat. × *C. lutetiana* L. subsp. *quadrisulcata* (Maxim.) Asch. & Magnus.—A. Upper and lower portions of flowering stem.—B. Flower; note exserted nectary.—C. Node of upper stem.—D. Inflorescence. From *Boufford & Wood 19717* (KYO, MO).

arising from the base, these most commonly opposite or subopposite and subtended by reduced leaves or leaflike bracts. The terminal raceme, from the uppermost reduced leaf or leaflike bract, to 15 cm long at cessation of flowering; the lateral racemes to 11 cm long at cessation of flowering, subequal to variable in length on the same plant. Flowering pedicels 1.7–2.3 mm long, perpendicular to the axis of the raceme, subglabrous to, more commonly, glandular pubescent with hairs as on the raceme axes, most commonly with a minute setaceous bracteole to 0.4 mm long at the base. Fruiting pedicels very rarely developing. Buds glabrous to pubescent, with short, capitate and clavate-tipped, glandular hairs ca. 0.1 mm long; pink or purple; oblong to very broadly elliptic in outline, rounded to acuminate at the apex; from the summit of the ovary, 2.8–4.7 mm long, 1.6–1.8 mm thick just prior to anthesis. Ovary 1–1.3 mm long, 0.6–1 mm thick at anthesis, obovoid to pyriform, densely pubescent with soft, translucent, uncinate hairs. Floral tube 0.6–0.8 mm long, ca. 0.2 mm thick at the narrowest point, funnelform, glabrous or pubescent with hairs as on the buds. Sepals 2.3–3.7 mm long, 1.4–1.8 mm wide, glabrous or pubescent abaxially with hairs as on the buds; pink or purple; oblong to oblong ovate, rounded or acuminate to the obtuse apex, reflexed in flower. Petals 1.8–2.5 mm long, 1.8–3 mm wide, most commonly wider than long, white or pink, obovate to transversely broadly obovate in outline; the apical notch 0.8–1 mm deep, ⅓ to nearly ½ the length of the petal; the petal lobes rounded. Stamens spreading at anthesis, shorter than the style; filaments 1.7–2 mm long; anthers 0.6–0.8 mm long, 0.5–0.6 mm thick. Style erect, straight, 3.2–3.9 mm long, topped by a transversely oblong, bilobed stigma, 0.3–0.4 mm tall, 0.5–1 mm thick. Nectar-secreting disc present as a low ring at the summit of the floral tube, 0.1–0.3 mm tall, ca. 0.5 mm thick. Mature fruit most often failing to develop, the ovaries aborting shortly after the falling of the hypanthium, when present, to ca. 2.5 mm long, to ca. 1.8 mm thick, pyriform, with or without shallow sulci, bilocular and 2-seeded, rarely both seeds fertile, densely covered with stiff, translucent, uncinate hairs. Combined length of pedicel and mature fruit, to ca. 9.5 mm long. Gametic chromosome number, $n = 11$ (9 bivalents plus a ring or chain of 4 at meiosis).

TYPE: Japan, Hokkaido, Hidaka-shicho, Samani-gun, Samani-cho, Okada, 21 August 1977, *D. E. Boufford & E. W. Wood 19717* (MO, holotype; CM, GH, K, KYO, MHA, MICH, NCU, NY, P, S, SHIN, UC, isotypes).

Distribution: Along streams in mixed deciduous or deciduous-coniferous forests. Known only from Hokkaido, Japan. Occurring below 200 m. Flowers, late July to late August.

Representative specimens examined:

JAPAN. HOKKAIDO: Hidaka-shicho, Samani-gun, Sumani-cho, Okada, *D. E. Boufford & E. W. Wood 19717* (CM, GH, K, KYO, MHA, MICH, MO, NCU, NY, P, S, SHIN, UC). Kushiro-shicho, Kushiro, Onbetsu. *M. Nakamura s.n.* (SAPS). Nikuppu, *S. Nogawa s.n.* (SAPS). One collection labelled only "Yezo" without further information (TI).

Circaea × *decipiens* (*C. erubescens* × *C. lutetiana* subsp. *quadrisulcata*) resembles *C.* × *dubia* (*C. cordata* × *C. erubescens*) but differs in several important features. *Circaea* × *decipiens* lacks the long, patent hairs found

in *C.* × *dubia* and *C. cordata* and is either glabrous or has only sparse pubescence on the stem below the inflorescence. The inflorescence bears only short, glandular hairs as in *C. lutetiana* subsp. *quadrisulcata*. However, in some plants of the hybrids, the glandular pubescence may be extremely sparse, which is never the case in *C. lutetiana*. The purple coloring of the buds and sepals is pronounced in *C. erubescens* × *C. lutetiana* subsp. *quadrisulcata* whereas in *C.* × *dubia* the buds and sepals are paler and may be white, green, or pink. The darkened nodes in *C.* × *dubia* are dull in appearance due to the often dense pubescence while in *C. erubescens* × *C. lutetiana* subsp. *quadrisulcata*, which has glabrous stems, the nodes are darkened and shining in live plants.

This hybrid differs from *Circaea erubescens* in having the petals more deeply notched, in having at least a few glandular hairs in the inflorescence and in having petal lobes that are rounded. From *C. lutetiana* subsp. *quadrisulcata* it differs in having the number of glandular hairs in the inflorescence often greatly reduced in density and in having the nodes conspicuously purple. A puzzling feature is that the nectar-secreting disc in the hybrid is often considerably shorter than in either parent. Another interesting feature of *C.* × *decipiens* is that, in some populations, the glandular hairs may be very dense on one raceme branch while nearly lacking on another on the same plant.

As with other hybrids in the genus, *C.* × *decipiens* needs some form of disturbance to become established. At Samani, Hokkaido, the hybrid grows approximately 50 m downstream from a mixed population of the two parents in an area subject to frequent disturbance from flooding, but at Kyoto University's Shibecha Experimental Forest no hybrids are found in an undisturbed deciduous forest despite the fact that *C. erubescens* and *C. lutetiana* subsp. *quadrisulcata* are abundant and grow intermixed.

Pollen fertility in *Circaea erubescens* × *C. lutetiana* subsp. *quadrisulcata* averages 8.2%, ranging from 4.4 to 8.8%, with mostly normal, 3-pored grains. One specimen labelled only "Hokkaido" ("Yezo"), and without collector or date (TI), and not included in the above averages, had all the pollen sterile in 355 grains examined.

Circaea erubescens Franchet & Savat. × *Circaea mollis* Siebold & Zucc.

Intermediate between *Circaea erubescens* and *C. mollis* but in habit often resembling one parent more than the other. Erect, 4–8 dm tall, simple or branched above, forming long, non-tuberous rhizomes which give rise to the following year's plants from their tips. Plants densely to sparsely pubescent; the stem with short, soft, falcately recurved hairs, 0.2–0.3 mm long; the inflorescence with a few capitate and clavate-tipped glandular hairs, ca. 0.2 mm long, and also with sparse falcately recurved hairs as on the stem, especially below; the petioles with sparse to dense falcate hairs as on the stem but these upwardly curved, these continuing along the main veins of the leaves or the leaves, except the margins, glabrous, leaf margins with short falcate cilia. Stem, green, the nodes purple. Leaves horizontally spreading, drooping at the tips, green or slightly reddened, opaque; those between the middle and the upper part of the stem the largest, 5–9 cm long, 2.7–4.5 cm wide, becoming gradually reduced in size upward and eventually bractlike and alternate in the lower part of the inflorescence; gradually reduced

in size downward; lanceolate to ovate lanceolate, not at all or only slightly acuminate at the apex, rounded at the base, denticulate to subentire, glabrous or pubescent with soft, short, falcate hairs, these most often restricted to the veins; leaf margins with short, falcate cilia ca. 0.2 mm long. Petioles 1–4 cm long, very sparsely to densely pubescent with upwardly curved, falcate hairs and a few straight hairs, ca. 0.2 mm long, with or without reduced branches arising in the axils. Inflorescence very sparsely pubescent with a few capitate and clavate-tipped, glandular hairs, ca. 0.2 mm long, occasionally with soft, falcately recurved hairs as on the stem, terminal on the main stem and at the tips of the uppermost reduced branches, less commonly arising also from the nodes, the branches commonly alternate, subtended by reduced leaves or leaflike bracts. The terminal raceme, from the uppermost reduced leaf or leaflike bract, ca. 2 cm long at initiation of flowering, to ca. 10 cm long at cessation of flowering; the lateral racemes 1–2 cm long at initiation of flowering, to ca. 7 cm long at cessation of flowering, subequal in length on the same plant. Flowering pedicels 1.6–3.5 mm long, perpendicular to the axis of the raceme, sparsely pubescent with a few glandular hairs, ca. 0.2 mm long, without or very rarely with a minute setaceous bracteole at the base. Fruiting pedicels developing to ca. 4.5 mm long before abortion of the fruit. Buds glabrous or glabrescent with glandular hairs ca. 0.1 mm long; green and often purple tinged or purple; oblong ovate to oblong obovate in outline, rounded to slightly acuminate to the obtuse apex; from the summit of the ovary, 2.5–2.9 mm long, 1.1–1.2 mm thick just prior to anthesis. Ovary 1.1–1.7 mm long, 0.8–1.1 mm thick at anthesis, obovoid, densely pubescent with soft, translucent, uncinate hairs. Floral tube 0.6–0.9 mm long, ca. 0.2 mm thick at the narrowest point, narrowly funnelform. Sepals 2–3.2 mm long, 1.2–1.4 mm wide, glabrous or glabrescent abaxially with hairs as on the buds; green or purple; oblong to oblong lanceolate, rounded or slightly acuminate to the obtuse apex, reflexed in flower. Petals 1.1–1.8 mm long, 1.2–1.6 mm wide, longer than wide, white or pink, obdeltoid to obovate in outline; the apical notch 0.3–0.6 mm deep, ¼ to slightly over ⅓ the length of the petal; the petal lobes truncate or rounded, occasionally minutely crenulate. Stamens spreading at anthesis, shorter than, to as long as the style; filaments 1.3–2 mm long; anthers 0.4–0.6 mm long, 0.4–0.5 mm thick. Style erect, straight, 2.2–3.4 mm long, topped by a usually prominently bilobed, obtriangular to transversely oblong stigma, 0.3–0.5 mm tall, 0.6–0.9 mm thick. Mature fruit developing to ca. 2.7 mm long, 1.9 mm thick, usually aborting shortly after the falling of the hypanthium, obovoid, with low ribs and shallow sulci, bilocular and 2-seeded, rarely the seeds fertile; densely covered with stiff, translucent, uncinate hairs, ca. 0.7 mm long. Combined length of pedicel and most mature fruit, 8.5 mm long. Gametic chromosome number, unknown.

Distribution: Roadsides, pastures and other disturbed habitats. Local and rare (?) on Hokkaido and Honshu, Japan.

Representative specimens examined:

JAPAN. HOKKAIDO: Mombetsu-gun, Tokinoue-cho, Oshira-neppu, *S. Okamoto s.n.* (KYO). HONSHU: SHIZUOKA PREFECTURE, Fujinomiya-shi, Mt. Fuji-san, Mura-kami, *I. Kato s.n.* (MAK 117770). TOCHIGI PREFECTURE, Nikko, *T. Makino s.n.* (MAK 6943, KANA). Bukojo to Takodate, *H. Fox s.n.* (BM). One collection labelled only "Japan, 20 July" (GH).

Circaea erubescens × *C. mollis* is intermediate between the two parents in several critical features but often, in overall appearance, resembles one parent more closely than the other, making identification difficult. The petals in the hybrid are more shallowly notched than in *C. mollis* and tend to have lobes that are often truncate or broadly rounded and minutely crenulate, reminiscent of *C. erubescens*. The nodes of *C. erubescens* × *C. mollis* are a deeper purple than in *C. mollis* but not as deep as in *C. erubescens*. The leaf bases are rounded in the hybrid and the leaves vary in shape from lanceolate to nearly ovate. The flowering pedicels in *C. erubescens* × *C. mollis* are nearly as short as in *C. mollis* and shorter than in *C. erubescens*. Familiarity with the parental species is extremely helpful in recognizing the hybrid.

The apparent rarity of *Circaea erubescens* × *C. mollis* is unexplainable. *Circaea erubescens* and *C. mollis* are the two most common and widespread species of the genus in Japan and China and often grow in close proximity to one another. Experimental attempts to produce this hybrid as well as further field work to locate additional popultions should be carried out.

Pollen fertility in *Circaea erubescens* × *C. mollis* averages 5.3%, ranging from 0% to 13.9%, with all normal, 3-pored grains.

Circaea × *mentiens* Boufford, hybrid nov. = *Circaea alpina* L. subsp. *alpina* × *Circaea erubescens* Franchet & Savat.—FIG. 31.

Circaea alpina L. subsp. alpinae simile, in nectario exsertio differt, et C. erubescentis Franchet & Savat. simile, in petalis profundioribus incisis ut in C. alpina differt.

Morphologically intermediate between *Circaea alpina* subsp. *alpina* and *C. erubescens*. Erect or decumbent at the base and rooting at the nodes, 1.2–3 dm tall, simple or, less frequently, branched above, forming numerous filiform rhizomes similar to those in *C. alpina* but never tuberous and only slightly thickened apically. Plants completely glabrous except for uncinate hairs on the ovaries and minute falcate cilia on the petioles and leaf margins. Stem green, the nodes purple, very conspicuously so in life and then appearing succulent. Leaves horizontally spreading, usually drooping at the tips, pale to dark green, nearly opaque to translucent; those near the summit of the stem the largest, 2.5–7 cm long, 1.7–4 cm wide; becoming very abruptly reduced in size at the base of the inflorescence and ultimately bractlike and alternate, gradually reduced in size downward; ovate to very broadly so, rarely subcircular, acute to short acuminate at the apex, truncate to cordate at the base, denticulate to prominently serrate; with minute, falcate cilia along the margins. Petioles 1.7–3.5 cm long, terete to subterete, glabrous or with upwardly curved, falcate cilia in lines along the upper surface. Inflorescence terminal on the main stem and less often at the tips of axillary branches; the racemes simple or branched at the base, the branches alternate, subtended by reduced leaves or leaflike bracts. The terminal raceme, from the uppermost leaf or leaflike bract, to ca. 10 cm long at cessation of flowering; the lateral racemes commonly shorter than the terminal but occasionally to 10 cm long, subequal to variable in length on the same plant. Flowering pedicels 1.5–3.2 mm long, perpendicular to the axis of the raceme to slightly ascending, the flowers opening after elongation of the raceme; with a setaceous bracteole, 0.2–

FIGURE 31. *Circaea* × *mentiens* Boufford (*C. alpina* L. subsp. *alpina* × *C. erubescens* Franchet & Savat.).—A. Mid-stem node.—B. Habit.—C. Flower with petal removed; note low exserted nectary.—D. Inflorescence. From *Boufford & Wood 19633* (CM, KYO, MO, SHIN, UC).

0.4 mm long at the base. Fruiting pedicels failing to develop. Buds elliptic to broadly so to ovate or obovate in outline, gradually rounded to short acuminate to the obtuse apex; from the summit of the ovary, 1.4–2.2 mm long, 0.7–1 mm long just prior to anthesis. Ovary 0.7–1 mm long, 0.3–0.7 mm thick at anthesis,

elliptic, clavate to obovate in outline, covered with soft, translucent, uncinate hairs. Floral tube 0.3–0.5 mm long, 0.1–0.2 mm thick at the narrowest point, funnelform. Sepals 1–1.7 mm long, 0.6–0.8 mm wide, white or pink; narrowly oblong, oblong lanceolate to broadly elliptic, gradually rounded to short acuminate to the obtuse apex, reflexed in flower. Petals 1.1–1.8 mm long, 0.8–1.4 mm wide, longer than wide, white or pale pink, narrowly obtriangular to broadly obovate in outline; the apical notch 0.2–0.4 mm deep, $^1/_5$–$^1/_3$ the length of the petal; the petal lobes rounded to obliquely deltoid. Stamens erect or spreading at anthesis, commonly equaling the style: filaments 0.7–1.4 mm long; anthers 0.4–0.5 mm long, ca. 0.3 mm thick. Style erect, straight, 1.5–2.2 mm long, topped by an obconic to transversely oblong, prominently bilobed stigma, 0.2–0.3 mm tall, 0.3–0.5 mm thick. Nectar-secreting disc present as a low, exserted ring at the summit of the floral tube, to 0.1 mm long, ca. 0.2–0.3 mm thick, more obvious in living plants. Mature fruits failing to develop, the ovary aborting shortly after anthesis. Gametic chromosome number, $n = 11$ (11 bivalents at meiosis).

TYPE: Japan, Hokkaido, Ishikari-shicho, Sapporo city, Mt. Maruyama, 17 August 1977, *D. E. Boufford & E. W. Wood 19633* (MO, holotype; CM, KYO, SHIN, UC, isotypes).

Distribution: Rocky stream margins and moist, naturally disturbed areas in temperate and mixed deciduous-coniferous forests. Hokkaido and Sado Island, Niigata Prefecture, Japan. From 20 to 200 m. Flowers, late July to mid-September.

Representative specimens examined:

JAPAN. HOKKAIDO: Abashiri-shicho, Yubetsu-cho, 1.6 km E of Engaru-cho on hwy 147, *D. E. Boufford & E. W. Wood 19795* (G, GH, K, KYO, MHA, MO, NCU, NY, S, SHIN). Iburi-shicho, Tomakomai Experimental Forest of Hokkaido University, *D. E. Boufford & E. W. Wood 19661* (KYO, MO). Ishikari-shicho, Sapporo city, Mt. Maru-yama, *D. E. Boufford & E. W. Wood 19633* (CM, KYO, MO, SHIN, UC). Tokachi-shicho, Hiro ("Forets d-Biro"), *U. Faurie 4842* (P). HONSHU: Niigata Prefecture, Sado Island, Aoneiba-goe, *F. Maekawa S113* (TI).

Based on past collections, *Circaea* × *mentiens* (*C. alpina* subsp. *alpina* × *C. erubescens*) appears to be rare and local in its occurrence. This assumption may be only partially correct for in the space of three weeks I was able to find three additional populations in three widely scattered areas on Hokkaido, Japan. The lack of more collections of this hybrid may be due largely to the fact that colonies of this plant often remain vegetative or produce only a very few inconspicuous flowering shoots. These non-flowering colonies are no doubt passed over as sterile plants of *C. alpina* subsp. *alpina* which the hybrid closely resembles.

Circaea × *mentiens* bears some resemblance to the hybrid *C.* × *intermedia* (*C. alpina* subsp. *alpina* × *C. lutetiana*) but the former has the leaves more distantly and evenly spaced and has a more spindly appearance as in *C. erubescens*. In *C.* × *mentiens* the leaves are not drastically different in size as they often are in other hybrids involving *C. alpina*, the nodes are a very deep reddish purple and very succulent and shining in living plants and the axis of the inflorescence is glabrous. Also, the branches of the inflorescence tend to be more lax and divergent as in *C. erubescens* rather than stiffly ascending as in other species and hybrids. The flowers in this hybrid are intermediate between the two parents.

The apical notch of the petals varies between being very shallow as in *C. erubescens* and moderately deep as in *C. alpina* subsp. *alpina*. A very low, ringlike nectary projects slightly above the opening of the floral tube. This latter feature is much more evident in living plants than in dried herbarium specimens where some shrinkage of the nectary occurs. The flowers in *C.* × *mentiens* open after the raceme axis elongates and are borne on rather loosely spaced, divergent to ascending pedicels.

The ovaries fail to develop in *Circaea* × *mentiens* and abort shortly after the falling of the floral tube. Pollen fertility averages less than 1% with mostly regular, 3-pored grains in plants examined.

Circaea × *intermedia* Ehrh., pro sp., Beitr. zur Naturkunde 4: 42. 1789. = *C. alpina* L. × *C. lutetiana* L.—FIG. 32.

Circaea lutetiana L. var. *intermedia* Hornem., Dansk Dec. Plantl. 25. 1806.
Circaea alpina L. β *major* Schrader, Fl. Germ. 1: 14. 1806.
Circaea lutetiana L. β *intermedia* (Ehrh.) Wahlenb., Fl. Suec. 1: 4. 1824.
Circaea × *intermedia* Ehrh. forma *inaequialta* Lasch, Linnaea 2: 446. 1827. TYPE: E. Germany, Neumark.
Circaea × *intermedia* Ehrh. forma *aequialta* Lasch, Linnaea 2: 446. 1827. TYPE: E. Germany, Neumark.
Circaea alpina L. β *intermedia* (Ehrh.) DC., Prodr. 3: 63. 1828.
Circaea lutetiana L. β *glabra* Soyer-Willemet, Obser. 151. 1828.
Circaea alpino-lutetiana G. Meyer, Chl. Hanover 100. 1836. Based on *C.* × *intermedia* Ehrh.
Circaea lutetiano-alpina G. Meyer, Chl. Hanover 101. 1836. Based on *C.* × *intermedia* Ehrh.
Circaea alpestris Wallroth, Fl. Hercyn. 109. 1840. Nom. subs., *C.* × *intermedia* Ehrh. in syn.
Circaea alpina L. β *sterilis* Döll, Rheinische Fl. 746. 1843. Nom. subs., *C.* × *intermedia* Ehrh. in syn.
Ocimastrum intermedium (Ehrh.) Rupr., Fl. Ingr. 368. 1860. Nom. subs., *C.* × *intermedia* Ehrh. in syn.
Circaea ericetorum Martrin-Donos, Bull. Soc. Bot. France 9: 130. 1862. TYPE: France, Dept. Tarn, Valence, among the heath ("Parmi les Bruyers").
Circaea × *intermedia* Ehrh. var. *minor* Grognot, Carian Cat. Pl. Saone-et-Loire 154. 1863.
Circaea lutetiana L. var. *intermedia* (Ehrh.) H. Lév., Monde des Pl. 7: 71. 1898.
Circaea lutetiana L. subsp. *intermedia* (Ehrh.) Rouy & Camus, Fl. Fr. 7: 204. 1901.
Circaea lutetiana L. subsp. *intermedia* (Ehrh.) Rouy & Camus β *ericetorum* (Martrin-Donos) Rouy & Camus, Fl. Fr. 7: 205. 1901.
Circaea lutetiana L. subsp. *intermedia* (Ehrh.) Rouy & Camus γ *minor* (Grognot) Rouy & Camus, Fl. Fr. 7: 205. 1901.
Circaea lutetiana L. race *intermedia* (Ehrh.) H. Lév., Bull. Acad. Int. Géogr. Bot. 22: 219. 1912.
Circaea lutetiana L. race *intermedia* (Ehrh.) H. Lév. forma *ericetorum* (Martrin-Donos) H. Lév., Bull. Acad. Int. Géogr. Bot. 22: 219. 1912.
Circaea canadensis (L.) Hill, sensu Fern., Rhodora 19: 85–88. 1917.
Circaea × *intermedia* Ehrh. forma *major* H. Lév. ex Hegi, Ill. Fl. Mit.-Eur. 5: 880. 1925.
Circaea × *intermedia* Ehrh. forma *minor* (Grognot) Hegi, Ill. Fl. Mit.-Eur. 5: 880. 1925.
Circaea × *intermedia* Ehrh. forma *bracteolata* H. Lév. ex Hegi, Ill. Fl. Mitt-Eur. 5: 880. 1925.
Circaea × *canadensis* (L.) Hill, sensu Fern. var. *rishiriensis* Hara, J. Jap. Bot. 34: 317. 1959. TYPE: Japan, Hokkaido, Rishiri Island, Oshidomari, August 1903, *T. Makino* (MAK 6954, holotype; TI, isotype).

Erect or decumbent at the base and rooting at the nodes, 0.7–4(–7) dm tall, simple or more commonly, branched above, very rarely bushy branched from near the base. Plants forming numerous and vigorous rhizomes, these occasionally giving rise late in the season to tuberous thickenings at the apex but most commonly the apical portion only slightly dilated; rhizomes also occasionally arising from the lowermost nodes of the stem and then arching and ultimately

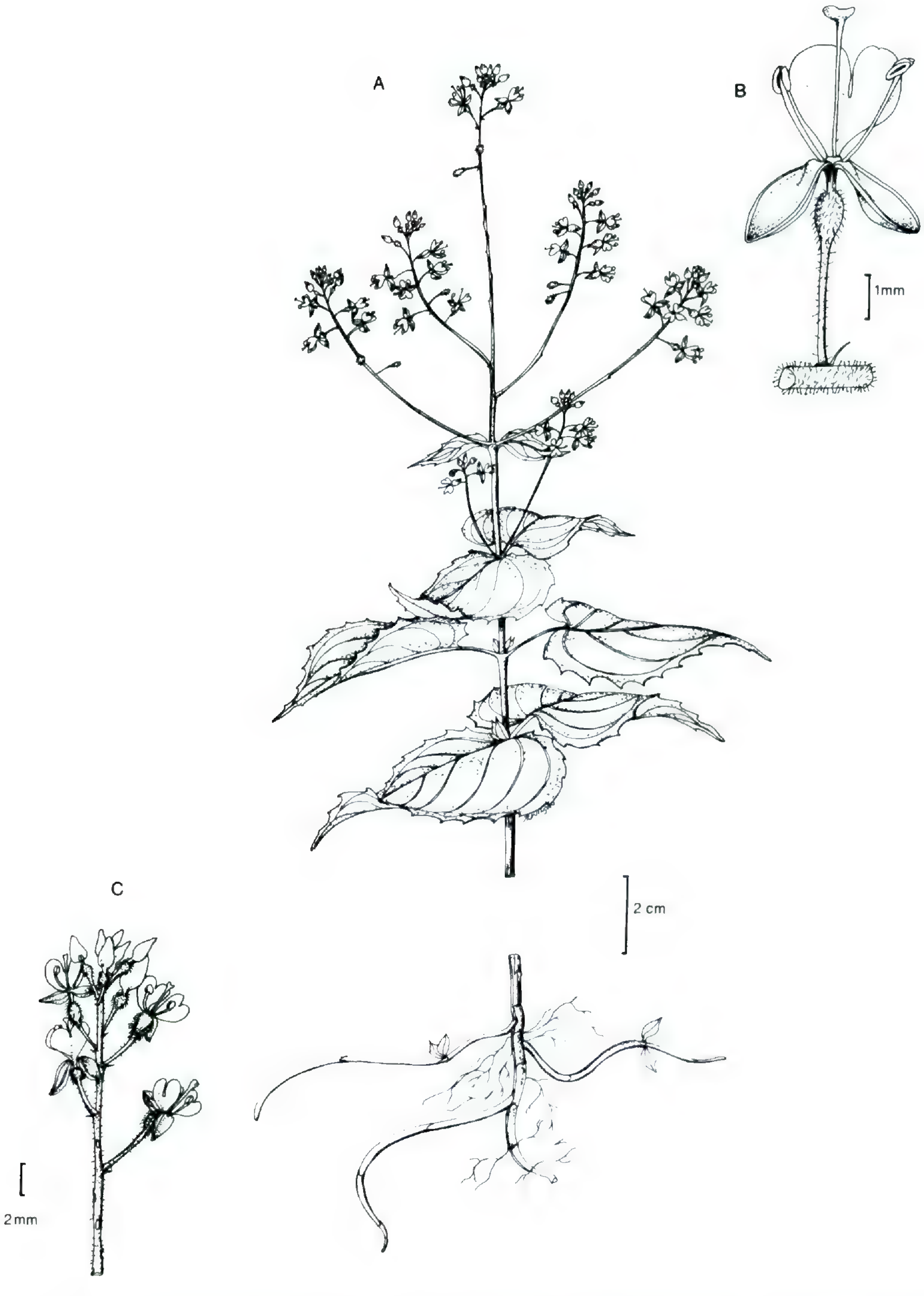


FIGURE 32. *Circaea* × *intermedia* Ehrh. (*C. alpina* L. subsp. *alpina* × *C. lutetiana* L. subsp. *canadensis* (L.) Asch. & Magnus).—A. Upper portion of flowering stem, roots—B. Flower with petal removed; note exserted nectary.—C. Inflorescence. From *Boufford 18829* (MO).

becoming subterranean, often the above ground portion giving rise to upright shoots from the nodes during the current growing season and often with the scalelike leaves enlarged and similar to the stem leaves; all rhizomes ultimately subterranean and giving rise to the following year's plants from their tips. Stem

glabrous or occasionally the nodes with a few soft, short, falcately recurved hairs, 0.2–0.3 mm long, less commonly the stem densely pubescent above with similar hairs. Axis of the inflorescence sparsely to densely pubescent with soft, short, capitate and clavate tipped glandular hairs. Petioles sparsely to densely pubescent in lines above with soft, short, upwardly curved, falcate hairs, these often continuing along the veins on the upper surface of the blade, and sometimes also on the interveinal areas, at least near the base, the leaf margins with slightly curved to falcate cilia. Stem green, commonly the nodes purple. Leaves horizontally spreading, drooping at the tips, pale to deep green but most commonly blotchy with irregular patches of pale and dark green, semi-translucent to opaque. Leaves from just above the middle to the summit of the stem the largest, 2–7(–11) cm long, 1.3–4.2(–7) cm wide, abruptly to gradually reduced in size upward to the base of the inflorescence and eventually bractlike and alternate, gradually to abruptly reduced in size downward; distantly to closely spaced, narrowly to broadly ovate, abruptly to gradually short acuminate to acute at the apex, rounded to cordate at the base, denticulate to prominently serrate. Petioles 0.8–5.5 cm long, terete or semiterete, sometimes flattened in pressing and appearing winged; pubescent in lines above with soft, short, upwardly curved, falcate hairs, 0.2–0.3 mm long; most often with reduced branches arising in the axils. Inflorescence sparsely to densely pubescent, with soft, short, capitate and clavate tipped, glandular hairs, 0.2–0.3 mm long; terminal on the main stem and a simple raceme or, more commonly, with one or more lateral branches arising from the base of the terminal raceme and from the tips of the short, uppermost axillary branches, less commonly at the tips of reduced branches arising from the lower axils; the lateral branches alternate or occasionally opposite, subtended by reduced leaves or leaflike bracts. The terminal raceme, from the uppermost reduced leaf or leaflike bract, ca. 1.5 cm long at initiation of flowering, to 18 cm long at cessation of flowering; the lateral racemes 1.5–3 cm long at initiation of flowering, to ca. 15 cm long at cessation of flowering, these equal or unequal in length on the same plant. Flowering pedicels 1.8–5.5 mm long, ascending at ca. a 45° angle to perpendicular to the axis of the raceme, glabrous to pubescent, with soft, short, capitate and clavate-tipped glandular hairs ca. 0.1 mm long; with a minute setaceous bracteole, 0.1–0.8 mm long, at the base. Fruiting pedicels developing to ca. 8 mm long before abortion of the fruits. Buds glabrous or, rarely, minutely and sparsely pubescent, with short glandular hairs ca. 0.1 mm long; white, pink or very pale green, commonly purple tinged at the apex; elliptic, oblong, oblong ovate to broadly obovate in outline, gradually tapering or short acuminate to the obtuse or minutely mammiform apex; from the summit of the ovary, 2–4.2 mm long, (0.7–)1–2.2 mm thick just prior to anthesis. Ovary 0.7–1.7 mm long, 0.5–1.1 mm thick at anthesis, fusiform, broadly ellipsoid to clavate or obovoid, densely covered with soft, short, translucent, uncinate hairs. Floral tube 0.4–1.2 mm long, 0.2–0.3 mm thick at the narrowest point, funnelform to very narrowly so, often the sides concavely tapering. Sepals 1.6–3.5 mm long, 0.9–2 mm wide, glabrous or glabrescent on the abaxial surface with hairs as on the buds, white, pink or pale green, commonly purple tinged at the apex, rarely purple throughout; narrowly oblong to oblong ovate or ovate, rounded to short acuminate to the obtuse or minutely mammiform apex; divergent to reflexed at anthesis. Petals

(1–)1.6–3.6 mm long, (0.6–)1.5–3.6 mm wide, longer than wide to as wide as long, white or pink, narrowly obtriangular to very broadly obovate in outline, cuneate to rounded at the base; the apical notch (0.4–)0.7–2.1 mm deep, (⅓–)½–¾ the length of the petal, the petal lobes rounded at the apex. Stamens erect or ascending, less commonly spreading at anthesis, as long as or slightly shorter than the style; filaments 1.3–3.7 mm long; anthers 0.4–0.7 mm long, 0.3–0.6 mm thick. Style straight, erect, 2.7–4.7 mm long; topped by an obtriangular to transversely oblong, often very prominently bilobed, stigma, 0.2–0.7 mm tall, 0.2–1.2 mm thick. Nectar secreting disc present as a low ring or cylindrical disc above the opening of the floral tube, 0.1–0.4 mm tall, 0.4–0.7 mm thick. Fruit sterile and aborting before maturity but occasionally developing to ca. 3 mm long and ca. 1.5 mm thick, clavate to obovoid, bilocular, often with one locule larger than the other, both containing infertile seeds; densely covered with stiff, translucent, uncinate hairs. Immature fruiting pedicels spreading perpendicular to the raceme axis or slightly reflexed. Combined length of pedicel and immature, sterile fruit developing to ca. 7.3 mm long. Gametic chromosome number, $n = 11$ (9 bivalents plus a ring or chain of 4 or 11 bivalents at meiosis).

TYPE: Germany, Diester Gebirge ("in Monte Diester"), *Ehrhart 101* (GOET, lectotype; L, W, isolectotypes).

Distribution (Figs. 33, 34): Moist places in deciduous, mixed or coniferous forests, especially in naturally disturbed areas along streams, occasionally as a weed in hedgerows and gardens in Europe. Central and western Europe, north to southern Scandinavia, southeast to E. Germany, Poland, Czechoslovakia, Austria, and Italy, west to southwestern France; British Isles; Caucasus Mountains; sporadically across Siberia to Far Eastern Asia; northeastern United States and southeastern Canada, westward to western Ontario, Minnesota, and Wisconsin; scattered in the Appalachian Mountains to North Carolina; disjunct in southwestern South Dakota. From sea level to ca. 1,800 m. Flowering, late June to late August.

Representative specimens examined:

NORTH AMERICA

CANADA. NEW BRUNSWICK: York Co., 1 mi. W of Keswick, *B. Boivin et al. 13337* (DAO, MT. TRT, UNB); Carleton Co., 2.5 mi. E of Hartland, *G. C. Cunningham in 1960* (DAO); Carleton Co., W of Woodstock, *W. Dore & E. Graham 45911* (ACAD, DAL, DAO, LL, MT, NHA); York Co., Upper Queensbury, St. John R., *M. L. Fernald & A. S. Pease 25204* (CAN, GH, MT, NY, US); Bass River (Nova Scotia?), *J. Fowler in 1875* (NY, US, WIS); Victoria Co., Salmon R., *G. A. Inch in 1892* (UNB); York Co., Crock's Point, St. John R., *P. R. Roberts 59-858* (UNB); Carleton Co., Hartland, *P. R. Roberts 60-256* (CAN); Victoria Co., Tobique R. at Arthurette, *P. R. Roberts & D. Drury 63-1212* (ACAD, UNB); Westmoreland Co., rte 30 W of Horewood, *P. R. Roberts & N. Bateman 64-2336* (ACAD, DAO, UNB); Kent Co., NNW of St. Anthony, Little Buctouche R., *P. R. Roberts & N. Bateman 64-2930* (UNB); Victoria Co., Tobique R. valley at Oxbow, *P. R. Roberts & B. Pugh 65-1123* (CAN, UNB); Kent Co., 1.5 mi. S of S St. Nicholas, W of St. Nicholas Bridge, *P. R. Roberts & B. Pugh 65-2304* (CAN, MT, UNB); Northumberland Co., 24 mi. W of Blackville, *P. R. Roberts & B. Pugh 65-3716* (CAN, UNB); Restigouche Co., mouth of Big Hole Brook at Jacquet R., *P. R. Roberts & B. Pugh 65-4833* (UNB); Kings Co., 1 mi. E of Rockville, *P. R. Roberts & B. Pugh 65-6454* (UNB); Kings Co., Sussex, *H. J. Scoggan 12354* (ACAD, CAN, MAK, W); York Co., Keswick, *E. Smith 19302* (ACAD); Carleton Co., 2 mi. SE of Hartland, *E. Smith & R. Clattenbug 20005* (ACAD); Albert Co., Pleasant Vale, *E. Smith et al. 20935* (ACAD); Carleton Co., Woodstock, *G. Stirrett in 1942* (DAO). NOVA SCOTIA: Kings Co., Kentville, *H. P. Bell 218* (DAL); Inverness Co.,

FIGURE 33. Distribution of *Circaea* × *intermedia* Ehrh. (*C. alpina* L. × *C. lutetiana* L.) In Eurasia.

Cape Breton Island National Park, 4 mi. E of Pleasant Bay, *W. Cody 21482* (DAO); Queens Co., Charleston, *J. Donly 1262* (ACAD); Pictou Co., Union Centre, *W. Dore & E. Gorham 45437* (ACAD, DAL, DAO, MT); Colchester Co., Great Village, *J. S. Erskine 51133* (ACAD, DAO, MT); Hants Co., bank of Meander R., *J. S. Erskine 52776* (ACAD, CAN); Hants Co., Five Mile River, *J. S. & D. Erskine 55529* (ACAD); Pictou Co., Salt Springs, *J. S. Erskine 55792* (CAN); Halifax Co., Upper Musquadoboit, *J. S. Erskine 51766* (ACAD, MT); Pictou Co., E of St. Mary, *J. S. Erskine 551154* (ACAD); Kings Co., Kentville, *M. L. Fernald in 1902* (GH), *H. Groh in 1930* (DAO); Pictou Co., Mt. Thom along rte 104, *M. J. Harvey in 1978* (DAL); Colchester Co., Stewiacke, along St. Andrews R., *M. J. Harvey in 1978* (DAL); Cumberland Co., Wentworth, Wallace R., *J. W. McLellan in 1938* (DAO); Kings Co., Kentville, *J. W. McLellan in 1938* (DAO, NA); Kings Co., Kentville, Farm Ravine, *H. Newcombe 11480* (ACAD); Cape Breton Island, *G. Nichols 732* (GH); Five Mile River, *A. S. Pease & B. Long 22004* (CAN, GH, PH); Hants Co., Five Mile River, *A. R. Prince & C. E. Atwood 1102* (DAO, DS, GH, MICH, WIS); Colchester Co., Truro, Salmon R., *A. R. Prince & C. E. Atwood 1410* (CAN); Cumberland Co., Centre Wentworth, *A. E. Roland 40580* (TRT); Inverness Co., Cape Breton, Cape North, *E. Scammon 4382* (GH); Cumberland Co., Wentworth, Wallace R., *W. Schofield 5271* (ACAD); Guysborough Co., Glenelg, *E. C. Smith et al. 527* (ACAD); Guysborough Co., N of Intervale, Guysborough R., *E. C. Smith et al. 659* (ACAD, DAO); Inverness Co., Hillsborough, *E. C. Smith et al. 999* (DAO); Victoria Co., Intervale forest, N Aspy R. Bridge, *E. C. Smith et al. 2703* (ACAD); Inverness Co., Judique, *E. C. Smith et al. 3956* (ACAD, DAO); Inverness Co., Melford, *E. C. Smith et al. 8728* (ACAD, CAN, MT, TRT); Pictou Co., West River, *E. C. Smith et al. 9871* (ACAD, MT, TRT); Antigonish Co., Crystal Cliffs, *E. C. Smith et al. 11563* (ACAD, TRT); Victoria Co., North River Bridge, *E. C. Smith et al. 14923* (ACAD, CAN, DAO); Antigonish Co., 2 mi. E of Purl Brook, *E. C. Smith et al. 17867* (ACAD); Queens Co., Mill Village, *E. C. Smith et al. 21278* (ACAD); Hants Co., Five Mile River near Latties Brook, *E. C. Smith et al. 21891* (DAO, UNB); Colchester Co., Kempton, *E. C. Smith et al. 23546* (DAO). ONTARIO: Ontario Co., Whitby,

FIGURE 34. Distribution of *Circaea* × *intermedia* Ehrh. (*C. alpina* L. × *C. lutetiana* L.) in North America.

L. V. Baker in 1915 (TRT); Ontario Co., Hamilton, *T. Burgess in 1888* (MTMG); Ottawa Dist., *M. Canfield in 1966* (KYO); Thunder Bay Dist., Crooks Twp, *Cormack & Mayall in 1936* (TRT); York Co., Toronto, Victoria College Grounds, *J. E. Cruise 78* (TRT); Thunder Bay Dist., Crooks Twp, Pine R., *C. E. Garton 2175* (CAS, DAO, GH, H, MIN, NY, RM, TRT, UC, US, W, WIN); Hastings Co., Marmora Twp, 3.5 mi. NE of Marmora, *J. Gillett 6485* (DAO); York Co., 2 mi. NW of Nobleton, 2 mi. E of Bolton, *E. Haber 553* (CAN, DAO, MICH, MTMG, NCU, TRT); Ontario Co., Swiss Chalet Park, N side of hwy 7 at Greenwood Pickering Twp, *E. Haber 558* (CAN, DAO, MTMG, NCU, TRT); Ontario Co., Pickering Twp, ca. 1 mi. N of Greenwood, *E. Haber 561* (CAN, DAO, MTMG, NCU, TRT); Peel Co., near Bolton, Cold Creek Swamp, *J. M. Hamley in 1959* (TRT); Waterloo Co., German Mills, *E. James 26439* (DAO, NA, TRT); Huron Co., 2 mi. NE of Bayfield, *P. Maycock & O. Maryniak 2842* (MTMG); Huron Co., Colborne Twp, 6 mi. N of Goderich, *W. Minshall 4764* (DAO); Algoma Dist., 10 mi. W of Sault Ste. Marie, *D. Ropke 531* (DAO); Wellington Co., Elora, Elora Gorge Conservation Area, *W. Stewart 1073* (DAO); Elgin Co., Union, *G. Stirrett in 1934* (DAO); Middlesex Co., Biddulph Twp, Lucan, *G. R. Thaler 286* (TRT); Huron Co., boundary Goderich-Stanley Twps, Varna, *G. R. Thaler 452* (TRT); NE Toronto, Dollar, *S. L. Thompson 290* (TRT); Waterloo Co., New Hamburg, *L. M. Umbach in 1899* (MIN); Waterloo Co., New Hamburg,

W. Umbach in 1894 (WIS); Rainy River Dist., Quetico Park, Three Mile Lake, *S. Walsh & D. Haddow 75-196* (CAN); Northumberland Co., Cobourg, *J. Young in 1919* (CU). PRINCE EDWARD ISLAND: Prince Co., Lower Freetown, *D. Erskine in 1967* (DAO); Prince Co., Seales Pond, *D. Erskine in 1975* (DAO). QUEBEC: Rimouski Co., Bic, *E. Bartram & B. Long 393* (PH); Huntington Co., 1.25 mi. SE of Franklin Center, *I. Bassett & A. Hamel 2581* (DAO); Megantic Co., Leeds Twp, at Osgoode R. bridge, *J. A. Bailey 1623* (V, mixed sheet with *C. lutetiana* subsp. *canadensis*); Matapedia Co., Matapedia, *R. Barabe in 1940* (DAO); Bonaventure Co.. Cascapedia, Cascapedia R., *R. & J. Cayouette 6350* (DAO); Gibraltar, Lake Memphremagog, *J. Churchill in 1902* (GH); Bonaventure Co., Nouvelle, Nouvelle R., *J. Collins & M. L. Fernald in 1904* (CAN, GH, MIN, MT); Harrington, *F. Cutten, in 1968* (MTMG); Richmond Co., Drummondville, *Fr. Euplius 525* (MT); Gatineau Park, near Luskville, *J. Gillett & G. Savage 15861* (CAN); Wolfe Co., Lingwick, Saumon R., *C. Hamel & S. Brisson 15407* (CAN, DAO, MTMG, SASK); Levis Co., Levis, Rang Sorosto, *C. Leduc L67-302* (TRT); Bonaventure Co., Nouvelle R., *E. Lapage 13427* (DAO); Compton Co., 0.5 mi E of Cookshire, *P. Maycock et al. 12793* (MTMG); Ancienne Lorette, near Petite R., *Fr. Marie-Victorin 15899* (CAN, GH, MT); Ancienne Lorette, Ruisseau d'Eau Claire, *Fr. Marie-Victorin 28417* (ACAD, CAN, DAO, GH, MT); Montmagny Co., Grosse-Ile, *Fr. Marie-Victorin 40019* (CAN, GH, IA, MT, NY); Montmorency Co., Montmorency, *Fr. Marie-Victorin et al. 44006* (CU, DAO, GH, MT, ND, TRT, UC); Bellechasse Co., Beaumont, *P. Masson 7624* (H); junction of Restigouche & Matapedia Roads, *J. Rousseau 32245* (CAN, DAO, MT, NY); Matapedia, Matapedia R., *J. Rousseau 32436* (CAN, DAO, GH, H, MT); mouth of Matapedia R., *H. Scoggan 908* (CAN); Sainte-Marie, *F. Stanislaus 566* (MT); Richmond Co., Ilverton, off Black R., *L. Terrill 7411* (DAO); Rimouski Co., Bic, Petite Portage, *C. Williamson in 1910* (PENN, PH).

UNITED STATES. CONNECTICUT: HARTFORD COUNTY, Bloomfield, along Farmington R., *C. A. Weatherby 4990* (NCSC, NEBC, PH); LITCHFIELD COUNTY, Kent, Falls Brook, *C. H. Bissell in 1921* (BHO), 1.2 mi E of rte 7 on rte 4, E of Cornwall Bridge, *D. E. Boufford & H. E. Ahles 18840* (MO), Cornwall, Cathedral R., *E. Hager 7317* (NEBC), Kent, *C. A. Weatherby 4950* (GH, NEBC); TOLLAND COUNTY, Union, *C. A. Weatherby 4772* (CAS, GH, NCSC, NEBC). MAINE: ARROSTOOK COUNTY, Fort Fairfield, Aroostook R. basin, *G. D. Chamberlain 2024* (UC), Fort Kent, St. John R., *E. Williams in 1900* (GH); CUMBERLAND COUNTY, Brunswick, *K. Furbish in 1891* (NEBC); FRANKLIN COUNTY, Farmington, *C. H. Knowlton in 1909* (NCSC, NEBC, NHA, WIS), *C. H. Knowlton in 1915* (PH, POM), Strong, *C. H. Knowlton in 1917* (PH); KENNEBEC COUNTY, Sidney, *M. L. Fernald & B. Long 14210* (GH, NEBC, NY, PH), Windsor, *M. L. Fernald 2628* (NEBC), Farmingdale, *C. H. Knowlton in 1917* (NCU, NEBC, PH) Winslow, *A. Norton 8840* (NHA); OXFORD COUNTY, Gilead, *A. S. Pease 17810* (NEBC); PENOBSCOT COUNTY, Pushaw Lake, *K. Furbish in 1891* (NEBC); PISCATAQUIS COUNTY, near Hunt's (near Katahdin), *A. Chute in 1847* (GH), Foxcroft, *M. L. Fernald 293* (CAN, GH, MASS, MIN, NEBC, NHA, NY, PH, US, WIS), trail to Hagas Gulf at Hay Brook, *F. C. Seymour 27910* (VT); SOMERSET COUNTY, Fairfield, *M. L. Fernald & B. Long 14209* (GH, NEBC, NY, PH), S of Bengham, Kennebec R., *W. E. Manning in 1934* (NEBC); WALDO COUNTY, Frankfort, *M. L. Fernald & B. Long 14208* (GH, ILL, NEBC, PH), Unity, *F. C. Seymour 30059* (VDB). MASSACHUSETTS: BERKSHIRE COUNTY, Sandisfield, ravine at Campbell Falls, *E. Hager 7948* (NEBC), Mt. Washington, Bash Bish Brook, *R. Hoffmann in* 1914 (NEBC), Sheffield, *R. Hoffmann in 1920* (NEBC); Bash Bish Falls, *F. Walters in 1913* (NHA); FRANKLIN COUNTY, base of Whately Glen, *W. E. Manning in 1930* (GH); WORCESTER COUNTY, New Braintree, Worcester, *B. Gates 31851* (NEBC, US). MICHIGAN: MARQUETTE COUNTY, Turin, *B. Barlow in 1901* (GH, NY, US). MINNESOTA: CARLTON COUNTY, Jay Cook Park, S of the St. Louis R., *O. Lakela 3746* (DAO, DUL, GH, MIN, TENN); CASS COUNTY, Lake Kilpatrik, *C. Macmillan & E. Sheldon 44* (ORE); LAKE COUNTY, outlet to Basswood Lake from Wind Lake, *O. Lakela et al. 16499* (DUL); ST. LOUIS COUNTY, S33, T49N, R15W, Magney Park, *E. Flaccus 10* (DUL), Duluth, below Superior Street bridge, *O. Lakela 1277* (DUL, MIN, NY, US), Fond du Lac, Mission Creek Valley, *O. Lakela 4195* (MIN), Duluth, Hunter's Hill, Tischer Creek bank, *O. Lakela 7847* (DUL), Crane Lake, Congdon Resort, *O. Lakela 13788* (DUL). NEW HAMPSHIRE: CHESHIRE COUNTY, Walpole, 3 mi. S of the junction of rtes 12 & 123 on 12, *D. E. Boufford 18851* (BM, C, CAS, CM, E, G, GH, K, KYO, LD, LE, MASS, MHA, MICH, MO, NHA, NCU, NY, P, PE, S, SHIN, UC), Alstead, *H. Noyes & M. L. Fernald 366* (GH, NEBC, NY); COOS COUNTY, Lancaster, *A. S. Pease 12827* (NEBC); GRAFTON COUNTY, above Plymouth, *M. L. Fernald 11819* (GH, NEBC); ROCKINGHAM COUNTY, Nottingham, Pawtuckaway Reservation, *A. R. Hodgdon & F. Steele 10742* (NHA); STRAFFORD COUNTY, Farmington, *C. W. T. W. in 1902* (NHA); SULLIVAN COUNTY, Plainfield, Sumner's Falls, *D. E. Boufford 4356* (KESC). NEW JERSEY: SUSSEX COUNTY, Montague Twp, *G. Nash in 1909* (NY). NEW YORK: CATTARAUGUS COUNTY, along Quaker Run, *W. Alexander & H. D. House 12332* (NYS); CAYUGA COUNTY, Genoa, Salmon Creek, *A. Eames 10508* (CU, IND); CHEMUNG COUNTY, Millport, bottom of Johnson Hollow ravine, *S. Smith 1439* (CU); CHENANGO COUNTY, Norwich, *M. H. Fitch s.n.* (POM); HAMILTON COUNTY, SE Benson Twp, Cole Hill, *E. Brundage et al. 4661* (NYS); NEW YORK COUNTY, Harlem Valley, *W. C. Twiss in 1918* (UT);

ONEIDA COUNTY, S of Utica, *J. Haberer 320d* (NYS); ONTARIO COUNTY, Canandaigua Lake, *Mrs. L. Ward in 1881* (US); RENSSELAER COUNTY, 3 mi. N of Nassau, *H. D. House 21767* (NYS); TOMPKINS COUNTY, Enfield, below Lucifer Falls, Enfield Ravine, *E. Dean & E. Eames 4636* (CU, GH), Ulysses, Taughannock Ravine, *A. Eames 8520* (CU, GH, IND, MICH, NYS), Ithaca, Enfield Gorge, *W. C. Muenscher & A. R. Bechtel 615* (CU, ISC, WS); WASHINGTON COUNTY, 2 mi. E of Vaughns, N of Hudson Falls, *S. H. Burnham in 1916* (BH, GH); WESTCHESTER COUNTY, Bedford, *N. L. Britton in 1900* (CM, RM). NORTH CAROLINA: SWAIN COUNTY, Cherokee Reservation, Qualla, *J. Mooney in 1888* (NCSC, US). OHIO: ASHTABULA COUNTY, Windsor Twp, 0.5 mi. S, U.S. rte 322, *L. W. Tandy 827* (VDB); GEAUGA COUNTY, Bainbridge Twp, *W. D. Hawver 1123* (KE); HOCKING COUNTY, Ash Cove, *E. A. Albaugh & L. Stephenson in 1930* (OS); HURON COUNTY, Collinswood, *S. Baldwin in 1888* (GH); TRUMBULL COUNTY, Casey's Spring, along Mill Creek, *D. E. Boufford 18822* (MO), above Mill Creek at Casey's Springs area, 2 mi. NNW of Mesapotamia, *T. S. Cooperrider 7924* (KE). PENNSYLVANIA: BLAIR COUNTY, 5.2 mi. N of Tipton, *W. E. Buker in 1972* (CM); CLINTON COUNTY, Lamar Twp, 3.6 mi. N of rte I-80 on rte 477, *D. E. Boufford 18831* (CM, KYO, MASS, MHA, MO), 2.5 mi. S of Rauchtown, along Antes Run, *W. F. Westerfeld 5175* (PAC, WIN); COLUMBIA COUNTY, 0.25 mi. NW of Central, *F. Fosberg 15985* (PENN); ELK COUNTY, Meddix Run, *O. E. Jennings & McClelland in 1925* (CM), Benezette Twp, *A. Rood & W. Simon 451* (PAC, PENN); FAYETTE COUNTY, Laurel Ridge at Ohiopyle, *J. Bright 9715* (SMU), *9716* (MIN), *9718* (DS), 1 mi. N of W. Va. line, Wymps Gap, Laurel Run, *O. E. Jennings & Lewis in 1940* (CM), 4 mi. SW of Ohiopyle, *O. E. Jennings in 1941* (CM), halfway between Ohiopyle & Dunbar, *O. E. Jennings in 1941* (CM); FOREST COUNTY, 1 mi. SE of Neiltown, *A. Shields D1957* (PAC); JEFFERSON COUNTY town of Sigel, 4.7 mi. SW of the junction of rtes 36 & 949 on 949, *D. E. Boufford 18825* (CM, KYO, MHA, MO), S of Allen Mills, 3.6 mi. N of rte I-80 on rte 310, *D. E. Boufford 18829* (BM, C, CM, E, G, GH, K, KYO, LD, MASS, MHA, MO, NCU, NY, PE, SHIN), along Mill Creek at rte 949, 5 mi. SW of Sigel, *L. K. Henry in 1952* (CM), 2.5 mi. S of Allens Mills, *L. K. Henry in 1953* (CM), along Clarion R. at Cooksburg, *O. E. Jennings in 1936* (CM); LACKAWANNA COUNTY, 1.5 mi. NNW of Dalton, *S. Glowenke 8869* (GH, PAC, PENN); LAWRENCE COUNTY, Rock Point, *O. E. Jennings in 1909* (CM), on the Connequenessing near Ellwood, *J. A. Shafer in 1900* (CM, PH), Chewton to Wurtemburg, *J. A. Shafer in 1900* (CM); LUZERNE COUNTY, North Mt. above Ricket's, *H. Meredith in 1920* (PENN); LYCOMING COUNTY, at Barbours, *H. A. Wahl 13565* (PAC, PENN), Pine Creek, 1.75 mi. ENE of Cedar Run, *H. A. Wahl 17690* (CU, GH, ISC, NCU, PAC, PENN), Little Pine Creek at English Center, *C. Wood, Jr. 1539a* (PENN); MCKEAN COUNTY, 1 mi. WNW of Eldred, *J. Fogg et al. 19831* (PENN), 1.25 mi. N of Derrick City, *J. Fogg et al. 19877* (PENN), Mt. Jewett, *O. E. Jennings in 1922* (CM); MONROE COUNTY, just W of Canadensis, *I. Langman 1118* (PENN); PIKE COUNTY, 2.5 mi. NE of Milford, *P. DePue 447* (BH, PENN); POTTER COUNTY, 4 mi. S of Coudersport, *C. E. Shaw in 1958* (CM), 2 mi. NW of Walton, *C. Wood, Jr. 1719* (PENN); SCHUYLKILL COUNTY, Neuremberg, valley of Big Tomchicken Creek, *A. E. Ortmann in 1909* (CM); SULLIVAN COUNTY, North Mountain, *D. Meredith in 1920* (PH); SUSQUEHANA COUNTY, Susquehana, Conowacta Creek, *S. Glowenke 9880* (NYS, PENN), Camp Susquehannock near Montrose, *L. Sowden in 1927* (PH), Elk Knob, 3 mi. N of Elkdale. *H. Wilkens 4794* (PAC); TIOGA COUNTY, Stony Fork Creek, *F. Trembley 181* (PENN); VENANGO COUNTY, 2.5 mi. S of Cranberry, *L. K. Henry in 1954* (CM); WARREN COUNTY, Allegheny National Forest S of Warren, *A. L. & H. N. Moldenke 27333* (LL); WESTMORELAND COUNTY, Powdermill Nature Reserved, Calverly area, *L. K. Henry in 1957* (CM). SOUTH DAKOTA: PENNINGTON COUNTY, Grizzly Bear Creek near Keystone, *H. E. Lee 480* (SDU), Grizzly Bear Creek, *H. E. Lee 499* (RM). VERMONT: ADDISON COUNTY, Ripton, Moosalamo Mt., *E. Brainerd in 1903* (VT), Salisbury, *E. Brainerd in 1903* (VT), *W. W. Eggleston 3281* (CM, DS, GH, NY, VT), Lake Dunmore, *T. Hope in 1917* (NEBC); BENNINGTON COUNTY, Manchester, *M. Day 363* (GH, NEBC, US, VT); CHITTENDEN COUNTY, *without collector in 1896* (VT); FRANKLIN COUNTY, Swanton, *C. H. Knowlton in 1931* (IND, NEBC), *C. H. Knowlton in 1932, Pl. Exs. Grayanae 571* (BH, BHO, CAS, COLO, CU, DAO, DS, DUKE, GA, GH, IA, ILL, ISC, KANU, LL, MASS, MICH, MIN, MONTU, MT, NA, NCSC, NCU, NEBC, NHA, NO, NY, NYS, PAC, PENN, PH, POM, RM, SMU, TENN, TEX, TRT, UARK, UC, UMO, US, UTC, WIS, WS, WTU, WVA. Specimens distributed as this collection at CAN & VT are *C. lutetiana* subsp. *canadensis*); LAMOILLE COUNTY, Morristown, *C. H. Knowlton in 1917* (ASU, NEBC, PH); WINDHAM COUNTY, Guilford, *S. K. Harris 23244* (NEBC), Townsend, *L. Wheeler in 1922* (NEBC); WINDSOR COUNTY, Royalton, *W. W. Eggleston 2573* (ILL, MIN, NY). VIRGINIA: BEDFORD COUNTY, Hales Fork, ca. 1 mi. below Camp Kewannee, Apple Orchard Mt., *R. S. Freer in 1933* (LYN), WEST VIRGINIA: FAYETTE COUNTY, near Thayer, *W. M. Grafton & C. McGraw in 1967* (WVA); RANDOLPH COUNTY, along Gandy Creek S of Whitmer at Swallow Rock, *R. B. Clarkson 3115* (WVA), mouth of Glade Run, Shavers Fork, *R. & J. Findley 158* (MAK), mouth of Whitemeadow Run, Shavers Fork, *R. & J. Findley 176* (CLEMS), Cheatbridge, *E. M. McNeill in 1948* (WVA), Winchester, Cheat R. clearings, *C. F. Millspaugh 737* (NY, WVA). WISCONSIN: ASHLAND COUNTY, S of Ashland, White R., *L. Cheney 4722* (WIS); BARRON COUNTY, Barron, *C. Goessl 8634* (B); BAYFIELD COUNTY, Fish Creek valley, *N. Bobb 770* (WIS); DOUGLAS

COUNTY, near St. Louis R. opposite Fond du Lac, *L. Cheney 7906* (WIS); IRON COUNTY, Ash Woods, Kimball Rd., *L. J. Uttal 12529* (VPI); LINCOLN COUNTY, Corning Twp, T31N, R5E, S17, *F. C. Seymour 15488* (SMU, WIS); OZAUKEE COUNTY, 1.6 km SE of Lake Church, along Lake Michigan, *H. H. Iltis 20301* (KYO); RUSK COUNTY, N of Strickland, Stony Brook, *N. C. Fassett 22044* (WIS).

EUROPE

AUSTRIA. S Tyrol, Gavardina Mts., *J. Ball in 1860* (IA); Gmunden, *S. Dörfler in 1887* (UC); Steiermark, Fedbach, Karbachtal, *H. Fleischmann s.n.* (W); at Durrbach near Ansdorf on Donan, *P. Fürst in 1903* (W); Burgstein, *P. Fürst in 1904* (W); near Adamstal near Brünn, *C. Hochstetter s.n.* (NA); Voralberg, Jagdberg near Schlins, *A. Neumann in 1967* (W); North Tirol, Oberes Inntal, Kronburg near Zams, *A. Polatschek in 1967* (W); N Tirol, Kössener Achental, between Kössen & Klobenstein, *A. Polatschek in 1972* (W); N Tirol, Oberintal, Schönwies, *A. Polatschek in 1972* (W); Steiermark, pagum Aussee, *K. & L. Rechinger 645* (DS, H, ND, W); Styria, Aussee, *K. Rechinger in 1928* (MO); Voralberg, Wolfurt near Bregenz, *R. Seipka in 1971* (W); Hallstatt, *O. Stapf, Fl. Exs. Aust.-Hung. 1273* (B, H, L, MIN, US, W).

BELGIUM. Warche valley near Beverce, *J. H. Kern & T. J. Reichgett 16629* (KYO).

CZECHOSLOVAKIA. Bohemia, Vernerice, Bobri valley, *B. Deylova in 1971* (H, KYO, NCU, UC); Gervont, Tatra, *A. Grzegorzk in 1884* (L); Trencin, *J. Holuby in 1875* (WA); Bohemia, Gratzen in Thiresienthale, *J. Jahn in 1888* (KSC); Bohemia, Gratzen, *J. Jahn in 1888* (W); Bohemia, Marianske e Lazne, Königswart, *J. Jahn in 1906* (W); Bohemia, E Moravia, opposite Vsetin, *G. Rican 1148* (CAS, DAO, DS, H, MO, MT, UC, W, WA); Bohemia, Sv. Marketa, *J. Trakal in 1947* (H, W); Bohemia, Teplice, *M. Winkler in 1853* (W).

DENMARK. Hellebaek, *M. Engstedt in 1910* (H); Kappel, Buchenwalder, *E. Fuchs in 1883* (RO); Hvalso, *J. Jefyresen in 1889* (TUR); Bornholm Island, *T. Jensen in 1866* (DS); Silkeborg, Vesterskov, *M. Lorenzen in 1893* (W); Jylland, Horsens, Silkeborg, Sönderskov, *J. Suominen in 1965* (H); Skov uid Skarid Sd., *Warming in 1896* (WS); Haslum Forest near Randers, *K. Wünstedt D13A* (KYO); Kolding, Jylland, *K. Wündstedt D25* (KYO).

FRANCE. Near Sarrebourg, *Baudot in 1868* (POM), *Baudot in 1838* (RO); Haute Savoie, Mt. Saxonnex, *E. Bourgeau s.n.* (CAS); Haute Savoie, Brison, *E. Bourgeau in 1868* (DS); Haute Savoie, *E. Bourgeau in 1869* (B); Colmars, *Boutignay in 1848* (DS); Isere, La Riviere, near la cascade du Versoud, *J. Cortey 2723* (MT); Haute Savoie, St. Nicolas la Chapelle, *Delavan in 1863* (DS); Yonne, Avallon, *G. Desplantes in 1928* (DS), *G. Desplantes 2383* (B, MT); Alsace, Strasbourg Botanical Garden, *J. Gardner 1330* (MT); Gavarnie, *Gavelle in 1963* (DAO); Nievre Dept., Mt. Sanche, *Gillot in 1883* (MT); Cantal Dept., forests of Claux, *E. Jordan 1684* (L); Cantal Dept., forests of Lioran, *E. Jordan 2146* (DS); Morvan, Cauelie valley, *S. Lassimonne 693* (US); Pringy, *Luget in 1867* (MO); Berhe, Laprugne, *M. Migout in 1875* (MT); Isere, Grande-Chartreause, *A. Pellat in 1889* (MIN); Isere, Uriage & St. Pierre-de-Chartreause, *A. Pellat 4886* (DS, MT); Savoie, Vallarasson near Queige, *E. Perrier in 1865* (MO, UC); Vasages Dept., Chiefosse, *L. Perrin in 1874* (DS); Cantal Dept., forests of Claux, *J. de Puyfol 1684* (MA, MT, W); Mt. Dore, forests of Capucin, *St.-Lager in 1885* (DAO); Mosalle, Bitche, *F. Schultz s.n.* (UC); Wissembourg, Lauter valley, *F. Schultz 476* (DS, H, W); Haute Savoie, Benneville, Mt. Brizon, *J. Timothee in 1865* (L); Champagney, *X. Vendechy in 1867* (DS); Champagney, Bahin valley, *C. Venosely in 1867* (DAO); Lavoie, Tulle, *Wilezek in 1921* (OKL).

GERMANY, EAST. Sachsen, Dresden, *Aitzss? in 1883* (CAS); Sachsen, Dresden, *H. Beger in 1922* (B); Thuringen, Sobenstein, *H. Beger in 1922* (B); Thuringen, Ob. Saaltal, *J. Bornmüller in 1922* (B); Rügen, *Bothe Herb. in 1903* (B); Bornholm, Storefos, *Buchheim in 1957* (B); Ilsenburg, *L. & J. Buse in 1849* (L); Thuringen, Fröhl Wieder Kunft, *C. Haussknecht in 1892* (SMU); Erzgebirge, *E. Korb in 1919* (W); Allgau, Freiberg, *Kuhn in 1870* (NEB); Brandenburg, near Vernmitz, *O. Ladermann in 1925* (DAO); Brandenburg, Tribbel, Laüka by Steinmetz, *O. Lasbunam in 1925* (IDS); Brandenburg, Hernsdorf, near Glunicke, *C. Mueller & W. Retzdorff in 1878* (COLO, MIN, MTMG); Dresden, *Reichenbach s.n.* (NA, PH); Sachsen, *A. Schade in 1907* (MIN); Brandenburg, Berlin, *R. Schulz in 1902* (B); Neumark, Konigsberg, *R. Schulz in 1910* (B); Karl Marx Stadt (Chemnitz), *M. Weiker 492* (POM); Thuringen, near Leutenberg, *A. Werner in 1895* (MIN).

GERMANY, WEST. Bergisches Land, road to Herrenstrunden, Bergisch-Gladbach, *H. Andres 89* (WS); Schleswig-Holstein, N of Lütjenburg, *E. Boel et al. 262* (COLO, H); Holstein, near Malente, *F. Buchenau in 1896* (CAS); Zwalbach, *M. Dewes in 1904* (B); Elberfeld, *F. Eggev in 1891* (WA); Upper Bavaria, near Oberaudorf, vicinity of Trisslbades, *G. Eigner & Dr. Vollmann 625* (UC, WA); Schleswig, Kappeln, *E. Fuchs in 1883* (COLO); Oberhessen, Kr. Lauterbach, road to Hochwaldhausen, *H. Hupke in 1967* (COLO, MONTU); Kr. Lauterbach, Ilbeshausen, *H. Hupke in 1969* (H, MAK), *H. Hupke in 1971* (H, TUR); Bavaria, near Bamberg, *Lanz in 1909* (DAO, MT); W. Hartz Mts.,

Achtermannstal, S of Oker, *A. Leeuwenberg 1637* (SMU); Meinberg, *A. Prager s.n.* (CAS); Bavaria, near Wissemburg, *F. Schultz in 1859* (DAO, MT).

ITALY. Corno, San Primo Mt., *U. & C. Cedercreutz in 1957* (H); near Monterosso, *Dnty in 1875* (RO); Pescara, Abruzzo, *A. Kuntze in 1866* (H); near Verzuolo, *E. Paoletti in 1899* (GH); Cottian Alps, *E. Rostan in 1880* (L).

NORWAY. Vestfold, Sande hd., Berger, *J. Dyring in 1917* (COLO, SASK); Hordaland, Standebarm, *T. Lillefosse in 1940* (H).

POLAND. Bialostok ("Bialzstolkin"), *A. Cunnüchan in 1891* (L); Myslenice Dist., Lipnik, *J. Dobrazanska & A. Szymoniakowna, Pl. Pol. Exs. 350* (DS, KYO, L, MO, MT, US, WA); Lubon Wielke, *A. Donle in 1966* (KRA); Bukowa Gora, Kielce, Klonow, *K. Kaznowski in 1924* (POM); Swietokryzski Mts., *R. Kobewice in 1924* (WA); Szcrecino, Cieszyn, *W. Wojewoola in 1955* (KRA); Krackow, *without collector in 1852* (B).

SWEDEN. Västergötland, Hummeberg, Nygard, *E. Almquist in 1912* (ARIZ, CAS, DAO, MT); Bohuslan, Ödsmåls, *E. Almquist in 1946* (MT, W); Skåne, Degeberga, Forsakar, *E. Asplund in 1928* (MT); Skåne, Helsingborg, *G. Bågenholm in 1894* (MIN); Småland, Jönköping, *H. Carlson in 1889* (MO); Skåne, *E. Fries in 1857* (MO); Helsingborg, *R. Fristedt in 1866* (US); Skåne, Palskop at Helsingborg, *Gyllenstjerna s.n.* (W); Huskvarna, *C. Johansson in 1876* (H, TUR, W); Halland, *K. Larson in 1894* (MTJB); Sverge, Skåne, Båstad, *A. L. Legerström in 1913* (TEX); Skåne, Hallandås, Simontorp, *B. Lidforss in 1885* (MT); Smål, Huskvarna, *J. Lundequist in 1895* (MT), *J. Lundequist in 1897* (B); Stockholm, Våstahamnen, *F. Nilsson in 1926* (UC); Bohuslan, Foss Parish, Saltkällen, *F. Nordstrom in 1900* (SMU); Helsingborg, Pålsjö, *H. H. Ringius 521* (H, PH, TUR); Skåne, Pålsjö, *E. Skotte s.n.* (WTU); Västergötland, Kinnekulle, *A. Stalin in 1913* (DAO); Stockholm, *C. Thedenius in 1891* (NA); Skåne, Pålsjö near Helsingborg, *Wallengren in 1883* (MIN).

SWITZERLAND. Crana-Vergeletto, Onsernone Valley, *J. Bår in 1906* (Z); Vaud, Mts. of Bex, *Boissier Herb. 1898* (UC); Valais, Troistorrents, *S. Curchod & P. Hainard 7653* (C, H, RNG); Meyringen, *C. Fischer-Boster in 1873* (Z); above Bex, *C. Meissner in 1819* (US); Bern, Reichenbach near Meiringen, *C. Meissner in 1829* (US); Neuchatel, Bois Rond, *D. Mouthier s.n.* (MT); Valais, Vernayaz & Salvan, *J. G. S. s.n.* (Z); Brisen, *E. Schmid in 1916* (Z); Jura, Belchen district at Eptingen, *C. Simon in 1965* (CAS); Toggeliloch near Düdingen, *T. Taquet in 1922* (MT); Graubünden, Seewis, *K. Urmi-König in 1976* (MO); Schaffhausen, Schleitheim, *Vetter s.n.* (Z); Zurich, between Uberrüth & Oberegg, *W. Wernol in 1906* (MO).

UNITED KINGDOM: ENGLAND. Westmorland, Rydal, *J. Ball in 1838* (IA, MO); Westmorland, Windermere, *J. Ball in 1876* (US); Staffs, Oakamoor, Star Wood, *E. Edees 8812* (DAO); Warwickshire, SW Birmingham, Harborne, *C. M. Goodman in 1960* (NO); Westmorland, Rydal, *G. E. Martindale 607b* (MIN); Westmorland, Ullswater, Glencoyne Wood, *P. H. Raven 16223* (DS); Lancashire, E of Lake Coniston, *A. Wilmot in 1937* (DAO). IRELAND. Leitrim, Glenade cliffs, *W. Barton in 1913* (DAO); banks of Lough Erne, *J. Ball in 1837* (PH); Belfast, *J. Ball in 1837* (GH, MTMG). SCOTLAND. W side of Loch Lomond, *J. Ball in 1850* (US); Arran Co., Brodick, *I. W. Brown in 1857* (H); Midlothian, Edinburgh, Braid Hermitage, *A. Craig-Christie in 1881* (SHIN); Colinton, Edinburgh, *A. Craig-Christie in 1898* (SHIN); Perthshire, Glen Lochay, *A. Currie & H. Munro 787* (DAO); Midlothian, Edinburgh, Colinton Dell, *B. P. Donaldson 50* (NCU); Arran, *G. Forrest, Jr. in 1928* (W); Perth, banks of Loch Tay, *W. Gardiner in 1862* (W); Arran Island, Brodick, *A. E. Lomax in 1885* (DS); Perthshire, near Loch Tay, *A. E. Lomax in 1887* (MIN); Inverness, Arisaig, *M. McCallum-Webster 5572* (DS); Inverness, Glen Beasdale, *M. McCallum-Webster 5577* (DS); Perthshire, Glen Lyon, *M. McCallum-Webster 5676* (DAO, DS); Perthshire, Lowers, shores of Loch Tay, *M. McCallum-Webster 5677* (DAO, DS); Sutherland, Inchnadamph, *M. McCallum-Webster 5755* (RSA); Inverness, Kirkhill, *M. McCallum-Webster 5794* (DAO, DS); Brackla, edge of Loch Ness, *M. McCallum-Webster 8442* (MO); Inverness, just N of Tomich, *M. McCallum-Webster 18404* (MO); Inverness, Cannich Strathglass, *M. McCallum-Webster 18408* (MO); Lewiston, by Loch Ness, *M. McCallum-Webster 18419* (MO); Drumnadrochit, Dirach, *M. McCallum-Webster 18552, 18553, 18554* (MO); edge of Loch Ness, Aldowine, *M. McCallum-Webster 18581* (MO); Inverness, by R. Enrick, 1 mi. W of Drumnadrochit, *C. Townsend in 1947* (SMU). WALES. Merioneth, 0.25 mi. N of Llanymawddwy, *P. H. Raven & W. Condry 16297* (RSA); Merioneth, Llanbedr, *P. H. Raven & P. Benoit 16302* (DS); Merioneth, Dolgellau, *P. H. Raven & P. Benoit 16314* (DS); Carmarthenshire, Rhydygrocs, Cilycum, *I. Vaughn in 1953* (MT).

U.S.S.R.

GEORGIAN S.S.R. Osetiya, between Tkue & Koshehka, *A. & V. Brotherus 342* (H, *C. alpina* subsp. *alpina* and *C. lutetiana* subsp. *lutetiana* on same sheet). LATVIAN S.S.R. Perse R. valley,

Kokenhusen, *Bruttan 273* (MW): Friederichstadt, Windsheim, foot of Dina R. cliff, *P. Lackschewitz 7601* (MW). RUSSIAN S.F.S.R. Ural Mts., Sverdlovsk ("Katherinaburg"), *Clere in 1875* (GH); Sachalin, Yuznosakhalinsk ("Toyohara"), *T. Sawada in 1923* (TI); Kaluga Prov., Juchnev Dist., *A. K. Skvortsov in 1972* (MO); Sachalin, vicinity of Yuzhno-Sachalinsk, *V. N. Voroshilov 7348* (MHA). UKRAINIAN S.S.R. Zarkapatsk Prov., Tyachevskiy, Polaninski Mt., *K. N. Igoshina in 1949* (MW). (See also: Skvortsov, 1979, for further discussion and distribution of *C.* × *intermedia* in the Soviet Union.)

ASIA

JAPAN. HOKKAIDO: Rishiri Island, *U. Faurie 3533* (KYO, SAP).

Circaea × *intermedia* is a sterile hybrid between *C. alpina* subsp. *alpina* and all subspecies of *C. lutetiana* and is intermediate between the two parents in many ways. Vegetatively *C.* × *intermedia* generally resembles *C. alpina* subsp. *alpina* more closely but in size and morphology of floral parts it is often more similar to *C. lutetiana*. The numerous synonyms are evidence of the confusion that *C.* × *intermedia* has caused in the past. Raven (1963) has clarified the situation in the British Isles and has pointed out that the most useful character for separating *C. alpina* subsp. *alpina*, *C. lutetiana* and *C.* × *intermedia* is the nature of the inflorescence. In *C. alpina* subsp. *alpina* the flowers are held in terminal corymbiform clusters on erect or ascending pedicels at the tip of the raceme. The flowers open before the axis of the raceme elongates. In *C. lutetiana* the axis of the raceme elongates before the flowers open. The flowers are held on pedicels that are distantly spaced and held perpendicular to the axis of the raceme. The flowers of *C.* × *intermedia* open as the raceme elongates and are held on ascending to spreading pedicels that are intermediate in spacing between the two parents. A low nectar-secreting disc is present in *C.* × *intermedia* but is less conspicuous than in *C. lutetiana*. An exserted nectary is absent in *C. alpina*. A bracteole is present at the base of the pedicel in *C.* × *intermedia*, *C. alpina* subsp. *alpina* and *C. lutetiana* subsp. *canadensis*. Bracteoles are very rarely present in *C. lutetiana* subsp. *lutetiana* and *quadrisulcata*.

Circaea × *intermedia* is vegetatively more vigorous than either *C. alpina* or *C. lutetiana* and often forms large, dense colonies. It is highly probable that *C.* × *intermedia* has been able to increase its range, at least over short distances, by the breaking off and transportation of rhizomes either naturally through the action of water or through the activities of man. The latter may be at least partially responsible for plants appearing spontaneously in gardens and other cultivated areas where the rhizomes could be brought in with soil. Raven (1963) has also suggested that the presence of the hybrid in areas where either one or both of the parents is absent could be due to changes in climate since the last glaciation which have caused some habitats to become unsuitable for one or both parents, but still suitable for the hybrids. The ability of hybrids of *Circaea* to persist for many years can be inferred from situations in North America and Japan where hybrids can still be found growing in the same places where they were collected 50 to 100 years ago, even though they are nearly or completely sterile. That these plants are not the result of recent hybridization cannot be ascertained, but the absence of one or both parents where the hybrids occur tends to partially rule out that possibility.

Benoit (1966, 1975) has synthesized *Circaea* × *intermedia* artificially using *C. alpina* subsp. *alpina* as the pistillate parent. Attempts to produce the hybrid using

C. lutetiana as the pistillate parent have been unsuccessful. Benoit states that the artificially produced hybrids are more similar to *C. alpina* subsp. *alpina* morphologically but probably resemble closely some natural populations of *C.* × *intermedia*. Backcrossing to *C. lutetiana* results in plants that produce fruits (Benoit, 1975) but it is not known if these are fertile.

Despite the fact that three different subspecies of *Circaea lutetiana* are involved in the formation of *C.* × *intermedia*, it is usually impossible to say with certainty which subspecies is involved based on morphological characters. Plants of *C.* × *intermedia* from Europe occasionally have pubescent stems (as do plants of *C. lutetiana* subsp. *lutetiana*) but the plants from Asia and North America and the vast majority from Europe have glabrous stems. Petal shape is variable in *C.* × *intermedia* with some plants having petals that are slender and cuneate at the base as in *C. alpina* subsp. *alpina* while others have petals that are broadened and with rounded bases as in *C. lutetiana*.

Haber (1977) and Cooperrider (1962) have provided statistical evidence for the intermediacy of *C.* × *intermedia* between *C. alpina* subsp. *alpina* and *C. lutetiana* subsp. *canadensis* in Ontario and Ohio in North America. Based on chromatographic evidence, Weimarck (1973) has suggested the possibility of backcrossing and introgression in the three taxa in Sweden.

Circaea alpina L. subsp. *imaicola* (Asch. & Magnus) Kitamura × *Circaea repens* Wallich ex Asch. & Magnus.

Morphologically intermediate between *Circaea alpina* subsp. *imaicola* and *C. repens*. Erect, 2–7 dm tall, simple below the inflorescence. Plants densely pubescent; the stem with soft, short, falcately recurved hairs, ca. 0.2 mm long; the inflorescence with soft, short, capitate and clavate tipped, glandular hairs, 0.2–0.3 mm long, often with falcate hairs as on the stem intermixed, at least below; the petioles with hairs as on the stem but these upwardly curved; the leaves glabrescent to evenly and densely pubescent with short falcate hairs, ca. 0.1 mm long. Stem green. Leaves horizontally spreading, green, opaque to slightly translucent; those just above the middle of the stem the largest, 5–7 cm long, 2.5–4.8 cm wide; becoming gradually to abruptly reduced in size upward to the base of the inflorescence and eventually bractlike and alternate, gradually to abruptly reduced in size downward; ovate to broadly so, acute to short acuminate at the apex, rounded to subcordate at the base, denticulate to dentate, glabrescent to densely pubescent on both surfaces, the margins with short, falcate cilia, ca. 0.1 mm long. Petioles 1–4 cm long, pubescent, sometimes densely so, with soft, upwardly curved falcate hairs, 0.1–0.2 mm long. Inflorescence densely pubescent with short, capitate and clavate-tipped, glandular hairs, 0.2–0.3 mm long, these intermixed with and giving way below to short, falcately recurved hairs; terminal on the main stem and at the tips of short, lateral branches arising from near the base of the terminal inflorescence, simple or abundantly branched with numerous lateral racemes, the lateral branches subtended by reduced leaves or leaflike bracts. The terminal raceme, from the uppermost reduced leaf or leaflike bract, 0.8–1.5 cm long at initiation of flowering, to 14 cm long at cessation of flowering; the lateral racemes 0.5–3 cm long at initiation of flowering, to 8.5 cm long at cessation of flowering, subequal in length on the same plant. Flowering pedicels

1.5–3.8 mm long, ascending at approximately 45° angles to the axis of the raceme, pubescent, with a few, short, capitate and clavate-tipped glandular hairs, 0.1–0.2 mm long; with a setaceous bracteole, to ca. 0.3 mm long at the base; rather closely spaced, the flowers clustered near the apex of the raceme. Fruiting pedicels developing to ca. 4.8 mm long before abortion of the fruits. Buds glabrous or glabrescent with a few minute glandular hairs; oblong elliptic to broadly oblong in outline, rounded to the obtuse or minutely mammiform apex; from the summit of the ovary, 1.3–2.7 mm long, 0.8–1.5 mm thick just prior to anthesis. Ovary 1.2–1.4 mm long, 0.6–0.7 mm thick at anthesis, clavate to obovoid, sparsely to densely covered with soft, translucent, uncinate hairs. Floral tube 0.3–0.5 mm long, 0.15–2 mm thick, funnelform to broadly so. Sepals 1.4–2.3 mm long, 1–1.5 mm wide, glabrous, purple or pink (or white?), ovate to oblong ovate, rounded to the obtuse or minutely mammiform apex, spreading to slightly reflexed in flower. Petals 1.2–1.5 mm long, 1.7–2 mm wide, most commonly wider than long, pink (or white?), obdeltoid to broadly so to transversely broadly oblong in outline; the apical notch 0.6–0.7 mm deep, ½–¾ the length of the petal, the petal lobes narrowly to broadly rounded. Stamens spreading or ascending at anthesis, equalling or shorter than the style; filaments 1.2–1.7 mm long; anthers 0.3–0.4 mm long, 0.3–0.4 mm thick. Style erect, straight, 1.9–2.2 mm long, topped by an obconic to transversely oblong, bilobed stigma, 0.2–0.3 mm tall, ca. 0.3 mm thick. Nectary wholly within the floral tube. Mature fruit apparently not developing, the ovary enlarging to 1.8 mm long, 0.7 mm thick, before aborting, sparsely to densely covered with stiff, translucent, uncinate hairs ca. 0.3 mm long. Young fruiting pedicels horizontally spreading. Combined length of pedicel and most mature fruit, ca. 7 mm long.

Distribution: Known only from southwestern China. Between 1,800 and 3,200 m. Flowers, August to early October.

Representative specimens examined:

CHINA: SICHUAN: Pao-hsing Hsien, *K. Chu 3481* (BM, E). YUNNAN: Fen-shui-ling, *E. Maire 341/1913* (E); Ta-hai, *E. Maire 997* (BM, E); Ta-hai, *E. Maire in 1912* (G).

The plants that are here considered to be hybrids between *Circaea alpina* subsp. *imaicola* and *C. repens* are intermediate between those two species in several ways and have highly sterile pollen. In stature, they resemble *C. repens* most closely, but have the inflorescence more abundantly branched than in either of the parental species. The flowers in the hybrids are smaller than in *C. repens*, rather closely spaced and held on ascending, minutely glandular pubescent pedicels. In *C. alpina* subsp. *imaicola* the pedicels are erect to ascending and glabrous. In *C. repens* the pedicels are glandular pubescent and most commonly spreading at right angles to the raceme axis. The hybrid also has petals that are deeply notched as in *C. repens* but are often broader as in some plants of *C. alpina* subsp. *imaicola*.

Pollen fertility in *Circaea alpina* subsp. *imaicola* × *C. repens* averaged 13% in 674 grains examined with all normal, 3-pored grains.

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NOTE

NOMENCLATURAL CORRECTIONS IN THE GENUS *CAMISSONIA* (ONAGRACEAE)[1]

In the process of assembling a nomenclatural index to the genus *Oenothera*, Warren L. Wagner brought to my attention two nomenclatural problems in the genus *Camissonia*.

In my 1964 synoptic treatment of the genera of the tribe Onagreae (Brittonia 16: 276–288) I made numerous new combinations of species, then in *Oenothera*, with capitate stigmas and continuous sporogenous tissue, and placed them in the genus *Camissonia*. For *Camissonia chamaenerioides* only an indirect reference to the basionym was indicated (Brittonia 16: 285). The following new combination is indicated:

Camissonia chamaenerioides (A. Gray) Raven, comb. nov.

Based on *Oenothera chamaenerioides* A. Gray, Pl. Wright. 2: 58. 1853.

The second problem involves *Camissonia pubens*. In my 1969 revision of *Camissonia* (Contr. U.S. Natl. Herb. 37: 161–396) the basionym of *Camissonia pubens* was inadvertently excluded from the list of synonyms (p. 316), and therefore the combination was not validly published. The following new combination is necessary:

Camissonia pubens (S. Wats.) Raven, comb. nov.

Based on *Oenothera strigulosa* (Fisch. & Mey.) Torr. & A. Gray var. *pubens* S. Wats., Proc. Amer. Acad. Arts 8: 594. 1873.

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[1] I am grateful to Warren L. Wagner for bringing these problems to my attention, and to the National Science Foundation for supporting my studies on Onagraceae by means of a series of grants.

Index to Onagraceae in this Issue

Page numbers of major entries are in **boldface.** Synonyms are in *italics*.

Boisduvalia 741, 772, 787, 792, 793
  densiflora 772
  macrantha 797
  subulata 741–743, 772, 783, 797
Bourreria 765
Calylophus 772, 784, 793
  berlandieri 772, 783, 793, 799
  hartwegii 772, 799
Camissonia 773, 783, 793
  andina 773
  chamaenerioides 995
  cheiranthifolia 798, 800
  claviformis 773, 800
  ovata 773, 798
  pubens 995
  sceptrostigma 773
Carlostephania 825
  major 878
  minor 931
Circaea 756, 773, 782, 784–786, 788, 791–792, **825–827**
  alpestris 980
  alpina 807–808, 810, 812, 815–819, 821–826, **900–904**, 914–915, 965, 980, 990
    α fertilis 931
    α minor 931
    β intermedia 980
    β major 980
    β sterilis 980
  forma composita 931
  forma dentata 931
  forma pacifica 920
  forma ramosa 931
  forma simplicissima 931
  subsp. alpina 807–809, 813–817, 822–824, 829, 895, 901, 903–905, 910, 919, **931–959**, 961, 977, 979, 980, 990–991
  subsp. alpina × caulescens 977, 979
  subsp. alpina × C. lutetiana 979–980, 990
  subsp. angustifolia 808–810, 819–820, 822–823, 825, 828, 901–905, **910–915**, 961
  subsp. caulescens 808, 810, 815, 818, 822, 824, 895, 901–904, **905–910**, 914–915, 930–931, 958
  subsp. imaicola 808, 818–819, 822, 895, 901–903, 905, 910, 913, **915–919**, 930, 961, 991–992
  subsp. imaicola × C. repens 991
  subsp. micrantha 807, 809, 820, 822–823, 825–826, 901–905, 910, 913, 919, 920, 930, 957, **959–961**
  subsp. pacifica 807, 819, 822–823, 825, 829, 901–902, 905, 910, **919–931**, 957
  var. aleutica 931
  var. caulescens 820, 905
  var. himalaica 896
  var. imaicola 915
  var. intermedia 931
  var. pacifica 920
  var. pilosula 905
  alpino-lutetiana 980
  bondinieri 829
  canadensis 852
  canadensis sensu Fernald 980
  canadensis sensu Fernald var. virginiana 853
  cardiophylla 829
  caucasica 905
  caulescens 905
    forma ramosissima 931
    var. glabra 931
    var. pilosula 905
    var. robusta 905, 958
    var. rosulata 931
  cordata 773–774, 796, 807–808, 810, 813–815, 817–825, **829–837**, 841, 849–850, 895, 959, 961, 965–966, 968, 971–972, 974
    var. glabrescens 820, 837
    × C. erubescens 841, 850, 962, 965, 971–972, 974
    × C. lutetiana subsp. quadrisulcata 966, 968, 972
    × C. mollis 850, 968
  cordifolia 931
  coreana 841
    var. sinensis 841, 849
  decumbens 930
  delavayi 886
  ericetorum 980
  erubescens 796, 807, 815, 818–823, 825, 840–841, 850, **886–896**, 959, 962, 965, 972, 975, 977, 979
    × C. lutetiana subsp. quadrisulcata 972, 975
    × C. mollis 975, 977
  glabrescens 807–809, 813, 819, 821–825, **837–841**, 895
  imaicola 905, 915
    var. angustifolia 820, 823, 910, 914
    var. mairei 912, 914
  intermedia 813, 819, 900
    β glabra 980
  kawakamii 887
  kitagawae 815, 829
  latifolia 852
  lutetiana 774, 796, 807, 813, 819–820, 822, 826, 849, **850–852**, 900, 930, 959, 965, 975, 979, 983, 990–991
    β canadensis 756, 758, 762–764, 819, 852
    β glabra 876
    β intermedia 980
    forma albiflora 878
    forma aprica 878
    forma brevipes 878
    forma carneostyla 878
    forma cordifolia 876
    forma glaberrima 876
    forma hirsuta 878
    forma hirtopetiolata 878
    forma longipetiolata 878
    forma mediterranea 878
    forma ovatifolia 876

forma pseudocordata 878
forma quadrisulcata 872
forma rubriflora 878
forma truncata 878
forma umbrosa 878
race alpina 931
race erubescens 887
race erubescens var. mairei 819–820, 911
race intermedia 980
race intermedia forma ericetorum 980
subsp. alpina 931
subsp. canadensis 806, 809, 816, 819–820, 822, 824, 841, 851, **852–872**, 876, 885, 959, 990–991
subsp. intermedia 980
β ericetorum 980
γ minor 980
subsp. lutetiana 806, 808, 813, 817, 819–822, 824–825, 849, 851–852, **876–886**, 990–991
subsp. mediterranea 878, 885
subsp. quadrisulcata 806, 815, 819–820, 822, 824, 849, 851, **872–876**, 885, 895, 966, 968, 972, 974–975, 990
var. alpestris 931
var. alpina 931
var. atrosanguinea 878
var. brevipes 878
var. cordifolia 817, 876, 878
var. decipiens 878
var. erythrocalyx 878
var. glaberrima 878
var. hirsuta 878
var. intermedia 980
var. longipes 878
var. obscurata 878
var. ovatifolia 878
var. taquetii 841
var. typica 878
var. villosa 821, 878
subvar. cordifolia 878
lutetiana sensu C. B. Clarke 896
lutetiano-alpina 980
major 876
maximowiczii 873
forma viridicalyx 873
var. viridicalyx 873
micrantha 959
minima 931
minutula 915
mollis 807, 814–815, 818–819, 821–824, **841–850**, 876, 895, 959, 968, 971–972, 975, 977
var. maximowiczii 872, 876
var. ovata 968
mollis sensu Maximowicz 829
nemoralis 876
ovalifolia 876
pacifica 819, 920
pricei 915
pubescens 876
quadrisulcata 815, 872
var. canadensis 854
var. ovata 815, 968
racemosa 876, 931
var. alpina 931
var. lutetiana 876
repens 807–808, 813, 819, 821, 823–826, **896–900**, 902–903, 991, 992
C. × canadensis sensu Fernald var. rishiriensis 980
C. × decipiens 807, 972
C. × dubia 815, 816, 820, 849, 962, 965, 971, 974–975
C. × dubia var. makinoi 815, 905
C. × hybrida 814, 820, 829
C. × intermedia 806, 809, 813–815, 817, 829, 895, 979, 990–991
C. × intermedia forma aequialta 980
C. × intermedia forma bracteolata 980
C. × intermedia forma inaequialta 980
C. × intermedia forma major 980
C. × intermedia forma minor 980
C. × intermedia var. minor 980
C. × mentiens 807, 829, 977, 979–980
C. × ovata 815, 849, 968, 971–972
C. × skortsovii 807, 966, 968
C. vulgaris 876
Clarkia 741–742, 744, 784, 787, 793
concinna 774, 793
imbricata 740
purpurea 774
rubicunda 774, 800
unguiculata 774
Epilobium 741–744, 771, 783, 787–788, 791–793, 801
angustifolium 742–743, 775, 783, 792–793
canum 775
coloratum 775
consimile 775
dodonaei 775, 792, 797
fleischeri 775, 792
glabellum 797
hirsutum 740
hornemannii subsp. behringianum 775
latifolium 775, 792–793, 797
leptophyllum 783
minutum 740, 774
oreganum 775, 783
paniculatum 741
pyrricolophum 797
Sect. Chamaenerion 775, 792
Sect. Cordylophorum 792
Sect. Crossostigma 775
Sect. Epilobium 775
Sect. Zauschneria 775
suffruticosum 775, 792–793
Fuchsia 749, 753–754, 760, 767, 770–771, 782–784, 786–788, 791–792, 806, 808
arborescens 776, 784
boliviana 776
decidua 755, 757–758, 760–762
fulgens 737
lycioides 776, 784
magellanica 749, 752
parviflora 776
procumbens 776

ravenii 776
thymifolia 749, 776
Gaura 771, 776, 782–783, 787–788, 791, 793–794
angustifolia 777, 782
biennis 777
demareei 777, 782
lindheimeri 777, 783, 793, 799
longiflora 777, 793
parviflora 782–783, 793, 799
Sect. Gaura 793
Sect. Schizocarya 793
suffulta 777, 783, 799
villosa 783, 799
Gayophytum 744, 746, 777, 793
diffusum 745
heterozygum 777
racemosum 745
Gongylocarpus 771, 777, 782, 787–788
rubricaulis 778, 793, 798
Hauya 771, 778, 782–784, 786–788, 792
elegans 778, 783, 792
Heterogaura 744, 778, 782, 786, 793
Lopezia 736, 749, 753–754, 779, 783, 786–788, 791–792, 806, 808
gentryi 779
grandiflora 779, 792
langmaniae 779
miniata 779, 783
nuevo-leonis 779, 801
ovata 779
racemosa subsp. racemosa 765, 796
riesenbachia 792, 796
semeiandra 796
suffrutescens 755, 757, 762–763, 765, 782, 784, 792
Ludwigia 736, 739, 741, 753, 755–756, 758, 764, 770–771, 774, 782–783, 786–789, 791–792
bullata 756, 759
elegans 756, 759
erecta 780
lagunae 780, 784
leptocarpa 780, 787
longifolia 756
maritima 780
octovalvis 759
palustris 780
peploides 780
peruviana 756, 759, 779–780, 786, 791
pilosa 780
polycarpa 780, 786
sedoides 780
sericea 756, 758, 761, 764
suffruticosa 779–780, 786
tomentosa 756, 759
Sect. Humboldtia 791
Sect. Ludwigia 791
Sect. Macrocarpon 791
Sect. Myrtocarpus 791
Sect. Oligospermum 791
Sect. Seminuda 791
Mandragora officinalis 819
Ocimastrum 825
intermedium 980
minimum 931
verrucarium 876
Oenothera 741–742, 744, 748, 771, 780, 786–787, 791, 793
biennis 737
caespitosa 749
centauriifolia 781
deltoides subsp. howellii 756–758, 762
grandiflora 781, 793
grandis 781, 800
hookeri 781
macrocarpa 793
macrosceles 781, 783, 793, 800
mendocinensis 781, 793
rosea 740
scabra 781
Sect. Megapterium 794
strigulosa 995
Regmus 825
alpinus 931
lutetianus 878
Xylonagra 782, 793
arborea 756–760, 762, 782, 793

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This special issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN (Vol. 69, no. 1, 1982) is devoted to several papers on the systematics of the genus *Fuchsia* (Onagraceae). The large section *Fuchsia,* which contains such horticulturally important species as *F. corymbiflora, F. triphylla,* and *F. fulgens,* contains 61 species, about 60% of the entire genus. Paul Berry's monograph treats the section in detail; extensive descriptions of flowers, blooming periods, habitats, and distribution are given. These are supplemented with beautiful color plates of several species. In addition to traditional keys to all the species, principal morphological differences between similar species and hybrids are treated in table form.

CONTENTS

The Systematics and Evolution of *Fuchsia* Sect. *Fuchsia* (Onagraceae)
Paul E. Berry 1

Pollinator Maintenance vs. Fruit Production: Partitioned Reproductive Effort in Subdioecious *Fuchsia lycioides.*
Peter R. Atsatt & Phillip Rundel 199

The Mexican and Central American Species of *Fuchsia* (Onagraceae) except for Sect. *Encliandra.*
Dennis E. Breedlove, Paul E. Berry & Peter H. Raven 209

Index 235

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